

Does winter come? Predicting endodormancy induction in walnut trees.

Guillaume Charrier

▶ To cite this version:

Guillaume Charrier. Does winter come? Predicting endodormancy induction in walnut trees. 2021. hal-03065757v3

HAL Id: hal-03065757 https://hal.inrae.fr/hal-03065757v3

Preprint submitted on 24 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1	Does winter	come? l	Predicting	endodormancy	^v induction	in walnut trees	3.
---	--------------------	---------	------------	--------------	------------------------	-----------------	----

- 2
- 3 Running title: Predicting endodormancy induction in walnut trees
- 4
- 5 Guillaume Charrier¹
- ⁶ ¹Université Clermont Auvergne, INRAE, PIAF, 63000 Clermont-Ferrand, France
- 7 *: corresponding author
- 8 Email: <u>guillaume.charrier@inrae.fr</u>
- 9 Tel: +33 4 43 76 14 21
- 10 UMR PIAF, INRAE Site de Crouel
- 11 5, chemin de Beaulieu
- 12 63000 Clermont-Ferrand

14 Abstract

The initial date for chilling accumulation (D_{CA}) is often set arbitrarily using various rules and 15 leading to a tremendous variability between studies and sites. To test the relevancy of different 16 17 calculation rules, sequential models taking into account, or not, the negative effect of warm temperature) were optimized on 34 endodormancy release and 77 budbreak dates of walnut cv 18 Franquette across France. The flexible D_{CA} was more efficient than using functions that 19 20 compute negative chilling accumulation at warm temperature. Most of the D_{CA} tested provided an accurate fit to the calibration datasets for budbreak, but less for endodormancy release. 21 22 Among the rules, the DORMPHOT model, integrating temperature and photoperiod control on endodormancy induction, was the most efficient (RMSEP < 10 and 8 days for endodormancy 23 release and budburst, respectively). The projections of the best model under different climate 24 25 (current and RCP scenarii) revealed a tipping point at a mean annual temperature of 13.86°C, beyond which the advance in ontogenic development during ecodormancy does not compensate 26 the delay in endodormancy release. The relationships between climate variables and plant 27 phenological processes would help to predict future phenological cycles on a global scale. 28

Keywords: Budburst, Chilling, Dormancy induction, Endodormancy release, Forcing, *Juglans regia* L, Photoperiod, Phenology, Trees.

31 Introduction

In frost-exposed environments, deciduous trees have to timely adjust their phenology to 32 anticipate unfavorable conditions during the winter period. To avoid exposure to frost events, 33 meristems switch from an apparently active period to a 'dormant' period, characterized by the 34 inability to grow even under favorable conditions. In temperate species, bud dormancy is 35 divided into three stages depending on the inhibiting factor (Lang et al., 1987). During 36 paradormancy, other organs such as apical bud or leaves inhibit meristem growth. During 37 38 endodormancy, growth is inhibited by factors intrinsic to the bud ('endo') whereas during ecodormancy, growth is limited by environmental factors ('eco'). During the transition from 39 growth to dormancy, different phenological stages are visible (e.g. growth cessation, leaf fall, 40 lignification or budset), whereas others are cryptic (*e.g.* endodormancy induction and release). 41

In autumn, endodormancy release is under the control of decreasing temperature and photoperiod (Welling *et al.*, 2002; Arora *et al.*, 2003; Maurya & Bahlerao, 2017). After endodormancy is released, 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 & Körner, 2012). Process-based models using these variables as input have been developed to simulate the endodormancy release and budbreak dates (Caffarra *et al.*, 2011a; Chuine *et al.*, 2016).

In the context of global change, it is particularly critical to accurately predict future trends in warmer climates. Since the first empirical model describing the relation 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 at the coldest time of the year (*i.e.* January 1st or July 1st in the northern and southern hemispheres, respectively), these models provide accurate results. However, this type of model is not effective in regions with warmer winters,

where attempts have been made to grow temperate crop species (e.g. in North Africa, the 56 Middle East or South America; Balandier et al., 1993). In this context, temperate perennial 57 crops exhibit q lack of chilling and insufficient endodormancy release (Weinberger, 1950). The 58 process of endodormancy, and the related chilling accumulation, had therefore been introduced 59 into the models (Weinberger, 1956; Vegis 1964). Different chilling accumulation functions 60 have been developed, depending on the species. An important difference is the consideration 61 of a delaying effect on endodormancy release for warm temperature (e.g. Utah model; 62 Richardson et al., 1974) or not (e.g. Chilling hours; Weinberger, 1967). In recent decades, 63 naturally growing trees have also been affected by a reduction in chilling exposure throughout 64 65 winter, increasing interest in the endodormancy stage (Gauzere et al., 2019).

Two-step models, simulating endo- and ecodormancy stages, are now commonly used to predict budbreak dates (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 (D_{CA}) is usually set arbitrarily with various rules resulting in huge variability between studies (from late summer until late autumn). Four different concepts of D_{CA} were used (see Tab. S1):

Fixed date across years and locations: from 1 September (Chuine *et al.*, 2016) to 1
November (Weinberger, 1967) for the northern hemisphere,

Flexible date through a simple climatic threshold: critical temperature (*e.g.* date of first frost;
Landsberg, 1974) or photoperiod (Welling *et al.*, 1997),

Flexible date through a mathematic function using a single variable such as the date of
minimum chilling units computed by the Utah model (Richardson *et al.*, 1974),

Flexible date through a mathematic function using interacting variables (temperature and
photoperiod) simulating leaf fall date (Delpierre *et al.*, 2009) or endodormancy induction
(DORMPHOT; Caffarra *et al.*, 2011a).

By aggregating data from 1975 until 2019 in different orchards across France for *J. regia* cv Franquette, different computations were tested to simulate the effects of the onset of chilling accumulation D_{CA} on the predictive accuracy of endodormancy release and budbreak dates. Specifically, we tested whether the use of dynamic D_{CA} 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 optimal model was evaluated for the prediction of future climate over France under three contrasting climatic *scenarii*.

88 Material and methods

89 Dormancy depth and endodormancy release

90 Endodormancy release dates were measured using the one-node-cutting 'forcing' test of 91 Rageau (1982). Sampling was performed every three weeks from October to March and 48 onenode cuttings were prepared per sampling date. Buds were isolated from other parts of plant to 92 93 avoid correlative inhibitions (Dennis, 2003). 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 94 top or less than 1 cm below the upper end, for terminal and axillary buds, respectively. For 95 axillary buds, the top of the cutting was covered with paraffin to prevent desiccation. The bases 96 of the cuttings were immersed in tap water, changed weekly. Forty-eight cuttings were exposed 97 to optimal conditions for growth resumption (i.e. 16/8 hours Day/Night and 25°C constant) and 98 observed individually every 3 days. Mean time until budbreak (stage 09 BBCH; Meier, 2001) 99 was computed from individual time until budbreak for each cutting. After endodormancy 100 release, buds of J. regia cv Franquette break out after 20 days under optimal conditions 101 (Mauget, 1980; Charrier et al., 2011). The endodormancy release dates were therefore obtained 102 by linear interpolation between the two dates giving a time to budbreak greater than (or equal 103 to) and less than (or equal to) 20 days, respectively. 104

105 Budbreak dates

Budbreak in the field was monitored every two to three 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.

109 *Climatic data*

The models were fit using the daily average and minimal temperatures observed by the weather 110 stations, mostly located in the same orchard and within 10km distance (Tab. 1). For prediction, 111 temperatures, calculated according to the CNRM-ALADIN52 model and corrected by a Q-Q 112 method (Déqué et al., 2007), were used from 8462 sites across France (Safran grid at 64km² 113 spatial resolution; MétéoFrance). Four datasets were used as input variable: the reference period 114 (1950-2005) and three contrasting climate scenarii (RCP 2.6, RCP 4.5 and RCP 8.5) for the 115 116 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 year. 117

- 118 Endodormancy induction and onset of chilling accumulation
- 119 The initial date for chilling accumulation (D_{CA}) was computed using different functions:
- 120 i) Fixed date as a Julian Day.
- ii) Flexible date based on threshold values reached by minimum temperature (T_{min}), mean
 temperature (T_{mean}), first frost (FF) or photoperiod.
- iii) Date of minimum chilling units (CU_{min}) computed according to the Utah model (originally
 developed on *Prunus persica* L. Batsch) which computes the negative chilling effect for
- temperature above 16°C (Richardson *et al.*, 1974). Daily CU were summed from DOY 182
- 126 (1 July) until DOY 365 (31 December) using the Utah_Model function (ChillR package;
- 127 Luedeling, 2019) as follows:

128
$$CU[\theta(t)] = \begin{cases} 0if\theta(t) < 1.4\\ 0.5if1.5\theta(t) < 2.4\\ 1if2.5 < \theta(t) < 9.1\\ 0.5if9.2 < \theta(t) < 12.4\\ 0if12.5 < \theta(t) < 15.9\\ -0.5if16 < \theta(t) < 18\\ -1if\theta(t) > 18 \end{cases}$$
(1)

129 with $\theta(t)$ the daily mean temperature.

iv) Predicted leaf fall dates (BBCH 97) 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 P_{start} and for a temperature colder than a threshold T_b , the variable R_{sen} , modulated by a photoperiod function in the case of the LFPT model, is summed up to a critical value (Y_{crit}), corresponding to the leaf fall date. Both LFT and LFPT models were computed using the original or optimized parameter sets: LF(P)T_{ori} and LF(P)T_{adj}, respectively.

137
$$R_{sen}[\theta(t); P(t)] = \begin{cases} 0ifP(t) \ge P_{start} \\ 0if\theta(t) \ge T_b \\ [\theta(t) - T_b]^2 \times \left(1 - \frac{P(t)}{P_{start}}\right)^y if\theta(t) < T_b \end{cases}$$
(2)

with θ(t) the daily mean temperature and P(t) the photoperiod. The parameter y was set to 0 and
2 for LFT and LFPT models, respectively.

v) The endodormancy induction state (DS) was computed according to the DORMPHOT
model developed for *Betula pubescens* Ehrh. by Caffarra *et al.* (2011a). The two sigmoidal
response functions to low temperature and photoperiod interact to compute DS. When ΣDS
reaches D_{crit}, the date is reported as D_{CA}. Both the original (DP_{ori}) and optimized (DP_{adj})
parameter sets were used.

145
$$DS[\theta(t); P(t)] = \frac{1}{1 + e^{aD(\theta(t) - bD)}} \times \frac{1}{1 + e^{10(24 - P(t) - DL_{crit})}}$$
(3)

with $\theta(t)$ the daily mean temperature, P(t) the photoperiod, aD a coefficient for the effect of temperature, bD a critical temperature and DLcrit a critical photoperiod. From D_{CA} , the effect of chilling temperature was simulated according to the inverse of the Richardson function (Richardson *et al.*, 1974). This function was defined as the best function predicting endodormancy release dates in walnut trees, although it does take into account the negation of chilling at warm temperature (Chuine *et al.*, 2016; Charrier *et al.*, 2018). According to the sequential paradigm, the date at which CU(t) reaches the critical CU_{crit} threshold (arbitrary chilling units, CU) is the date of endodormancy release (D_{ER}), or the transition from endodormancy to ecodormancy:

156
$$CU(t+1) = CU(t) + Max[Min(T_{high} - \theta(t); T_{high} - T_{low}); 0]$$
(4)

with CU(t) the chilling unit on day t, T_{high} the temperature above which CU(t) is 0 and T_{low} the temperature below which CU(t) is maximum; CU(t) is linear between T_{low} and T_{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.*, 2010).

$$162 \qquad CU(t+1) = CU(t) + \begin{cases} \frac{1}{1+e^{-4\frac{\theta(t)-T_{m1}}{T_{opt}-T_{m1}}}} \text{ if } \theta(t) > T_{m1} \\ \frac{1+e^{-4\frac{\theta(t)-T_{m1}}{T_{opt}-T_{m1}}}}{(T_{m1}-T_{opt})^2} \text{ if } T_{m1} < \theta(t) < T_{opt} \\ \frac{1-(1-\min)\frac{0.5(\theta(t)-T_{opt})^2}{(T_{m1}-T_{opt})^2}}{(T_{m1}-T_{opt})^2} \text{ if } T_{opt} < \theta(t) < T_{n2} \\ \min + \frac{1-\min}{1+e^{-4\frac{T_{n2}-\theta(t)}{T_{n2}-T_{opt}}}} \text{ if } T_{n2} < \theta(t) \end{cases}$$
(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 *Topt* which has half the efficiency of *Topt* to release endodormancy; min the effect of warm temperature to delete previously accumulated CU. 167 The ontogenetic development during ecodormancy stage was modeled according to a 168 sigmoid function (Caffarra *et al.*, 2011a). The date when FU(t) reaches the critical threshold 169 FU_{crit} (arbitrary forcing units, *FU*) is the budburst date (D_{BB}).

170
$$FU(t+1) = FU(t) + \frac{1}{1 + e^{-slp(\theta(t) - T_{50})}}$$
(6)

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

173 Model calibration depending on the onset of chilling accumulation

174 For a given D_{CA} rule, endodormancy release date was calibrated first and the best set of parameters was used to calibrate the bud break date. The nls function (using Gauss-Newton 175 algorithm, R ver.3.6.2; R development Core Team, 2019) was used to minimize the sums of 176 square between the observed and predicted values with different sets of starting values at the 177 minimum, average and maximum ranges of realistic parameter values. In order to maximize the 178 variability within the datasets, half of the observation per site was assigned to the calibration 179 dataset, the other half to the validation dataset. Two independent calibration procedure were 180 performed using symmetrical datasets. For an odd number of observations per site, one more 181 observation per site was included in the calibration set #1. 182

For the endodormancy release model, in addition to the parameters defining D_{CA} , three parameters were optimized: T_{Iow} and T_{high} corresponding to the temperature thresholds and CU_{crit} the sum of chilling units to release endodormancy.

For the ecodormancy model, one parameter was optimized: FU_{crit} corresponding to the sum of forcing units for bud break. The endodormancy model used to predict D_{ER} was the best from the previous step and the other parameters (slp and T₅₀) set to the values described in Charrier *et al.* (2018). The quality of the fit and predictive ability of the models in relation to the D_{CA} were assessed
for calibration and validation datasets by computing Root Mean Square Error (RMSE),
Predictive Root Mean Square Error (RMSEP) and Akaike Index Criterion (AIC_C):

193
$$RMSE(P) = \sqrt{\frac{\sum_{i=1}^{n} (\hat{y}_i - y_i)^2}{n}}$$
 (7)

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

195
$$AIC_{c} = 2n \left[log(RMSE) + \frac{k}{n-k-1} \right]$$
(8)

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

197 Correlations between simulated and climate variables

Correlations between the mean endodormancy onset date, mean endodormancy release date (D_{ER}) and mean budbreak date (D_{BB}) per site (8462 sites at 64km² 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 AIC_C.

203 **Results**

204 Dormancy stages

During the endodormancy induction stage, the time to bud break generally increased by 20 days between August and October and reaches a maximum value (50-80 days) between October and December (Figure 1). The endodormancy release is observed when the time to bud break gradually decreased to 20 days. The transition from endodormancy to ecodormancy is marked by a breaking point in the curves between mid-December and mid-February. Significant correlations were observed between the onset of endodormancy and the date of maximum depth of dormancy (P = 0.005; Fig. 1B) and between the date of maximum depth of dormancy and the date of endodormancy release (D_{ER} ; P = 0.030; Fig. 1C). However, no correlation was

observed between the onset of endodormancy and D_{ER} (P = 0.387; Fig. 1D).

214 *Effects of D_{CA} on endodormancy release date*

215 The use of different rules to compute the initial date for chilling accumulation (D_{CA}) had a relatively small effect on the prediction of D_{ER} (Tab. 2). The use of a positive chilling function 216 217 was overall more efficient than functions that take into account the delaying effect of warm temperature (positive and negative). For most rules, 75% of the RMSEs were within 2-3 days: 218 between 11.5 and 13.3 days and between 7.2 and 9.5 days for dataset #1 and #2, respectively. 219 However, the uses of FF and CU_{min} ori were not effective for both datasets. The predictive 220 ability was relatively good for most of the D_{CA}, with 75% RMSEP between 8.3 and 11.6 days 221 222 and between 12.9 and 14.4 days for dataset #1 and #2, respectively. Finally, considering the 223 rule that provided values below 125% of the minimum for RMSE and RMSEP in both datasets, only a few rules appeared satisfactory: Photoperiod and LFPT adj (positive only), CU_{min} adj 224 (positive & negative), LFPT ori, DORMPHOT ori and DORMPHOT adj (positive only and 225 226 positive & negative). By increasing the stringency to 110%, only DORMPHOT adj (positive only) could be considered an accurate and robust model. 227

228 Effects of D_{CA} on budburst date

The accuracy of the fits was slightly better for budbreak date (D_{BB}) than for D_{ER} (Tab. 3), 229 although the effect of the different rules on D_{BB} was relatively similar to that observed for D_{ER}. 230 The use of the positive chilling function was more effective than positive & negative functions. 231 For most of the D_{CA}, 75% of the RMSEs were within a 2-3 days range: between 7.4 and 9.6 232 233 days and between 6.8 and 8.6 days for dataset #1 and #2, respectively. The uses of FF and CU_{min} ori were also less efficient. The predictive ability was less than one week for most D_{CA}, with 234 75% of RMSEP between 6.7 and 9.3 days and between 6.9 and 8.2 days for dataset #1 and #2, 235 respectively. Considering the D_{CA} that had values below 125% of the minimum for RMSE and 236

RMSEP for both datasets, most of the rules, with the exception of FF and CU_{min} ori, appeared satisfactory. By increasing the stringency to 110%, several rules remained accurate and robust: Julian day and photoperiod, LFPT adj (positive only), LFT ori (positive & negative), LFPT ori and DORMPHOT ori (positive only and positive & negative). Finally, with the exception of FF and CU_{min} ori, all models provided relatively accurate phenological predictions for D_{ER} (RMSEP <15 days) and D_{BB} (RMSEP < 8 days), but DORMPHOT adj (positive only) can be considered the best.

244 Predictions under current and future climates for Juglans regia cv Franquette

DORMPHOT adj (positive only) was used to explore the current and future phenology trend. 245 D_{CA}, D_{ER} and D_{BB} have a structured geographical distribution across France (Fig. 2). D_{CA} 246 247 spanned a range of 43 days: earlier in the mountain areas (Mid-August) and later on the 248 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 249 of December in mountain areas to the end of February on the Mediterranean coast. D_{BB} showed 250 251 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. 252

D_{CA}, D_{ER} and D_{BB} were strongly correlated with the mean annual temperature (MAT), 253 although following different functions (exponential for D_{CA} and D_{ER} and cubic function for 254 D_{BB}; Fig. 3). Similar trends were observed in future climate predictions, with close relationships 255 between MAT and D_{CA}, D_{ER} or D_{BB} (Fig. 4). The functions describing the relationships between 256 257 MAT and D_{CA} and D_{ER} were monotonic. Warmer temperatures, as predicted by the different 258 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 259 (Fig. 4A; G). Consequently, endodormancy release would be delayed by 6-7 days until 2050 260 and, by the end of the century, by up to 24 days under the RCP 8.5 scenario (Fig. 4B; H). 261

However, the delay in the release of endodormancy did not directly affect the D_{BB}. The 262 263 relationship between D_{BB} and temperature shows a tipping point *i.e.* a temperature higher than 13.83°C would induce later D_{BB} (Fig. 3C). D_{BB} would occur only 3-4 days earlier until 2050 264 (Fig. 4C; I). By the end of the century, bud break is expected to be earlier under RCP 4.5 265 scenario (-6.4 days) than under the warmer RCP 8.5 scenario (-3.5 days). Finally, a later bud 266 break than today is likely to occur in an increasing portion of the France at the end of the 21st 267 century: from 5.6 (RCP 4.5) to 33.8% (RCP8.5) of the French territory in 2051-2100 (Fig. 5). 268 Considering the main French production areas, *i.e.* 'Noix de Grenoble' (Middle East) and 'Noix 269 du Périgord' (Middle West) Protected Designation of Origin (PDO) areas, bud break would be 270 271 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. 272

The current annual variability in phenological stages is similar for D_{CA} and D_{ER} (variance of about. 5 days; Fig 4D, E). The future climate would increase the variance in D_{CA} and D_{ER} considerably, especially for RCP 8.5 in the 2051-2100 period (about 10 days). However, the pattern is reversed for D_{BB} , with variance of 10 days in the current period, while 5-7 days are expected in the future climate (Fig 4F). In both PDO areas, the variance in D_{BB} would decrease by 2-3 days (RCP 8.5 scenario).

279 **Discussion**

The definition of the initial date for simulating cyclic processes is a key issue. To predict the annual phenological cycle in perennial organisms, such as trees, various empirical rules have been used so far. The onset of chilling accumulation during the endodormancy stage (D_{CA}) had, for instance, been arbitrarily set using fixed dates regardless of year and location (Chuine *et al.*, 2016) or depending of environmental factors controlling the induction of endodormancy (Caffarra *et al.*, 2011b). In the current study, long-term observations of phenological stages (endodormancy release D_{ER} and bud break D_{BB}) were used to define the most efficient rule under various environmental conditions. For most computations, the different rules for defining D_{CA} did not have a large impact on the accuracy of endodormancy release and bud break dates (*ca.* 2-3 days; Tab. 2-3). Overall, using a function that computes the negative effect of warm temperature, such as the Utah model, did not improve accuracy. Using a relevant D_{CA} is therefore more robust than negating early chilling accumulation in walnut in France as was also observed using a fixed D_{CA} date (Chuine *et al.*, 2016).

293 Across years and sites, the large ranges of variation for the date of endodormancy induction, date of maximum dormancy and date of endodormancy release (more than 2 month) suggest 294 that they cannot be predicted by a simple trigger such as a fixed date or photoperiod (Caffarra 295 296 et al., 2011a). Furthermore, the strong correlation between the onset of endodormancy induction (August - October) and the maximum depth of dormancy (October – December) indicates that 297 the duration of endodormancy is generally 2 month with a relatively small effect of 298 environmental conditions (Fig. 1). In contrast, the maximum depth of endodormancy and 299 endodormancy release are less correlated although significant, temperature being the main 300 301 driver of endodormancy release (Weinberger, 1959). However, it is not clear whether chilling 302 temperature actually acts only during endodormancy release or already during the induction of endodormancy. 303

304 The optimization of the different models showed that the different rules for defining the D_{CA} do not induce large variations in the predicting of D_{ER} and D_{BB} from September to November. 305 However, the date of the first frost event and the date of CU_{min} were less efficient than the other 306 rules. All relevant rules for dataset #2 considered a potential effect of photoperiod, either 307 directly or indirectly via the fixed date (Welling et al., 1997; Chuine and Régnière, 2017). The 308 309 DORMPHOT model, originally developed in *Betula pubescens*, is relevant for other deciduous species such as Juglans regia. The optimal date for chilling accumulation is in late summer 310 (mean date 28 August), suggesting that buds actually integrate information from chilling 311

exposure during budset although MTB is only beginning to increase. The use of a critical photoperiod (*e.g.* 12h observed on September 21^{st}) or a fixed date (*e.g.* 1 September; Chuine et al., 2016) is therefore relatively relevant, although it may be shifted by 20 days in the future climate (Fig. 4).

316 The conceptual development of the DORMPHOT model is based on experimental results combining the manipulation of photoperiod and temperature (Caffarra et al., 2011b), whereas 317 318 other formalisms were based on empirical observations (e.g. leaf fall; Delpierre et al., 2009). Temperature and photoperiod are closely correlated over the seasons. However, temperature 319 fluctuations are much larger at a given time of the year, which could induce greater variability 320 321 in the onset of endodormancy if it were the only controlling factor (Fig.1). As the induction of endodormancy is a lengthy process (ca. 2 month), perennial plants cannot rely solely on 322 temperature changes that may be too sudden to induce winter dormancy in time (Caffarra et al., 323 2011a). Photoperiod and temperature variables therefore affect the annual phenological cycle 324 of perennial plants, although to different extents in different species. For example, photoperiod 325 326 is dominant in Populus (Kalcsits et al., 2009) and Vitis (Fennel & Hoover, 1991), while temperature is dominant in Malus, Pyrus (Heide & Prestrud, 2005) and Sorbus (Heide, 2011). 327 The interaction between photoperiod and temperature has been demonstrated in Prunus (Heide, 328 329 2008). 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 330 al., 2005). 331

The rule selected for the D_{CA} predicted a delayed onset of chilling accumulation in warmer locations in France (> 7°C MAT; Fig. 3A). Warmer temperature indeed delays the induction of endodormancy in different species (Beil *et al.*, 2021). Such a delay would further delay the release of endodormancy (Fig. 3 B; Caffarra *et al.*, 2014; Chuine *et al.*, 2016). However, after endodormancy release, cold temperature would limit ontogenetic development during

ecodormancy, providing a negative spatial picture of D_{BB} compared to D_{ER} (Fig. 2B-C). Under 337 338 current climatic conditions, chilling requirements are generally fulfilled annually and therefore 339 play a minor role in D_{BB} variations (Gauzere et al., 2017). Using a sensitivity analysis with a fixed D_{CA} , Gauzere *et al.* (2019) also observed a minor role of D_{CA} in predicting D_{BB} only. 340 Comparison of the two phenological stages showed that the role of D_{CA} was more important in 341 predicting D_{ER} than D_{BB} (Tab.2-3). As many studies are based on D_B, only, without information 342 343 on D_{ER}, many different formalisms seem valid and are commonly used for phenological modeling (Tab. S1). However, the use of experimental results to fit phenological models is 344 essential to ensure that the fitted functions remain realistic (Chuine et al., 2016; Hänninen et 345 346 al., 2019). Finally, the D_{CA} simulated by the DORMPHOT model provided the most accurate predictions for D_{ER} and D_{BB} in both datasets. 347

Under future climate conditions as predicted by the RCP *scenarii*, the tipping point for D_{BB} 348 (MAT = 13.86°C) would be reached in a larger fraction of France. Above the 13.86°C threshold, 349 350 induction and release of endodormancy would be more delayed than ecodormancy hastened, 351 resulting in delayed bud break compared to the current period. Delayed bud break would thus cover up to one quarter of France under RCP 8.5 scenario in 2051-2100 (Fig. 5). Such a lack 352 of chilling during endodormancy has also been assumed for apricot in the UK (Martínez-353 354 Lüscher *et al.*, 2017). Interestingly, in the future climate, the annual variability in D_{BB} is expected to be lower. The trend towards a more uniform D_{BB} has already been observed in 355 recent decades (Vitasse et al., 2018). A more uniform phenology would act as a stabilizing 356 factor for fruit production by synchronizing pollination and ripening. However, the lack of 357 chilling temperature during endodormancy induces severe agronomic issues such as erratic 358 359 patterns of blooming, floribondity, and potential dischronism with anthesis (Campoy et al., 2011). An accurate assessment of temperature response during endodormancy is therefore 360 necessary to complement the experimental data obtained during the ecodormancy stqge 361

(Charrier *et al.*, 2011). It would clarify the future of the French walnut production area. The two PDO areas would indeed face distinct threats as they are on opposite sides of the tipping point. In the Périgord, chilling requirements are likely not to be fulfilled and varieties with lower chilling requirements need to be developed, 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, and varieties with higher forcing requirements can help stabilize production (Charrier *et al.*, 2018).

369 Conclusions and perspectives

This study highlighted the relevance of using flexible dates to initiate chilling accumulation 370 rather than functions that compute the negative chilling accumulation at warm temperature. The 371 DORMPHOT model, integrating the control of endodormancy induction by temperature and 372 photoperiod, is the most efficient in predicting endodormancy and ecodormancy stages. The 373 tipping point of phenological processes will probably be reached during the 21st century with 374 chilling requirements that are likely to be fulfilled later or not at all. Although these results are 375 important for walnut production, the observed correlation between MAT and phenological 376 stages represents a relevant tool for building meta-models valid in many species at the global 377 378 scale.

REFERENCES

- Arora, R., Rowland, L. J., & Tanino, K. (2003). Induction and release of bud dormancy in woody perennials: a science comes of age. *HortScience*, *38*(5), 911-921.
- Balandier, P., Gendraud, M., Rageau, R., Bonhomme, M., Richard, J. P., & Parisot, E. (1993). Bud break delay on single node cuttings and bud capacity for nucleotide accumulation as parameters for endo-and paradormancy in peach trees in a tropical climate. *Scientia Horticulturae*, 55(3-4), 249-261.
- Basler, D., & Körner, C. (2012). Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, *165*, 73-81.
- Beil, I., Kreyling, J., Meyer, C., Lemcke, N., & Malyshev, A. V. (2021). Late to bed, late to rise—Warmer autumn temperatures delay spring phenology by delaying dormancy. *Global Change Biology*.
- Caffarra, A., Donnelly, A., Chuine, I., & Jones, M. B. (2011a). Modelling the timing of Betula pubescens budburst. I. Temperature and photoperiod: a conceptual model. *Climate Research*, *46*(2), 147-157.
- Caffarra, A., Donnelly, A., & Chuine, I. (2011b). Modelling the timing of Betula pubescens budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate research*, *46*(2), 159-170.
- Caffarra, A., Zottele, F., Gleeson, E., & Donnelly, A. (2014). Spatial heterogeneity in the timing of birch budburst in response to future climate warming in Ireland. International journal of biometeorology, 58(4), 509-519.
- Campoy, J. A., Ruiz, D., & Egea, J. (2011). Dormancy in temperate fruit trees in a global warming context: a review. Scientia Horticulturae, 130(2), 357-372.
- Charrier, G., Bonhomme, M., Lacointe, A., & Améglio, T. (2011). Are budburst dates, dormancy and cold acclimation in walnut trees (Juglans regia L.) under mainly genotypic or environmental control?. *International journal of biometeorology*, *55*(6), 763-774.
- Charrier, G., Chuine, I., Bonhomme, M., & Améglio, T. (2018). Assessing frost damages using dynamic models in walnut trees: exposure rather than vulnerability controls frost risks. *Plant, Cell & Environment*, *41*(5), 1008-1021.
- Chuine, I., & Régnière, J. (2017). Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics*, 48, 159-182.
- Chuine, I., Bonhomme, M., Legave, J. M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A., & Améglio, T. (2016). Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology*, 22(10), 3444-3460.
- Delpierre, N., Dufrêne, E., Soudani, K., Ulrich, E., Cecchini, S., Boé, J., & François, C. (2009). Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. Agricultural and Forest Meteorology, 149(6-7), 938-948.
- Dennis, F. G. (2003). Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience*, *38*(3), 347-350.
- Déqué, M., Rowell, D. P., Lüthi, D., Giorgi, F., Christensen, J. H., Rockel, B., ... & van den Hurk, B. J. J. M. (2007). An intercomparison of regional climate simulations for Europe: assessing uncertainties in model projections. *Climatic Change*, 81(1), 53-70.
- Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., de Cortazar-Atauri, I. G., & Chuine, I. (2017). Integrating interactive effects of chilling and photoperiod in phenological processbased models. A case study with two European tree species: Fagus sylvatica and Quercus petraea. *Agricultural and Forest Meteorology*, 244, 9-20.

- Gauzere, J., Lucas, C., Ronce, O., Davi, H., & Chuine, I. (2019). Sensitivity analysis of tree phenology models reveals increasing sensitivity of their predictions to winter chilling temperature and photoperiod with warming climate. *Ecological Modelling*, *411*, 108805.
- Hänninen, H., Kramer, K., Tanino, K., Zhang, R., Wu, J., & Fu, Y. H. (2019). Experiments are necessary in process-based tree phenology modelling. Trends in Plant Science, 24(3), 199-209.
- Hänninen, H., & Tanino, K. (2011). Tree seasonality in a warming climate. *Trends in plant science*, *16*(8), 412-416.
- Heide, O. M. (2008). Interaction of photoperiod and temperature in the control of growth and dormancy of Prunus species. *Scientia Horticulturae*, *115*(3), 309-314.
- Heide, O. M. (2011). Temperature rather than photoperiod controls growth cessation and dormancy in Sorbus species. *Journal of experimental botany*, 62(15), 5397-5404.
- Heide, O. M., & Prestrud, A. K. (2005). Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. *Tree physiology*, 25(1), 109-114.
- Kalcsits, L. A., Silim, S., & Tanino, K. (2009). Warm temperature accelerates short photoperiod-induced growth cessation and dormancy induction in hybrid poplar (Populus× spp.). *Trees*, 23(5), 971-979.
- Landsberg, J. J. (1974). Apple fruit bud development and growth; analysis and an empirical model. *Annals of Botany*, *38*(5), 1013-1023.
- Lang, G. A., Early, J. D., Martin, G. C., & Darnell, R. L. (1987). Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. *HortScience*, 22(3), 371-377.
- Luedeling, E. (2019) Statistical Methods for Phenology Analysis in Temperate Fruit Trees, chillR Package.
- Martínez-Lüscher, J., Hadley, P., Ordidge, M., Xu, X., & Luedeling, E. (2017). Delayed chilling appears to counteract flowering advances of apricot in southern UK. Agricultural and Forest Meteorology, 237, 209-218.
- Mauget, J. C., (1980). Dormance et précocité de débourrement des bourgeons chez quelques cultivars de Noyer (Juglans regia L.).
- Maurya, J. P., & Bhalerao, R. P. (2017). Photoperiod-and temperature-mediated control of growth cessation and dormancy in trees: a molecular perspective. *Annals of botany*, *120*(3), 351-360.
- Meier, U. (2001). Growth stages of mono- and dicotyledonous plants. BBCH Monograph. doi: 10.5073/bbch0515.
- Mølmann, J. A., Asante, D. K., Jensen, J. B., Krane, M. N., Ernstsen, A., Junttila, O., & Olsen, J. E. (2005). Low night temperature and inhibition of gibberellin biosynthesis override phytochrome action and induce bud set and cold acclimation, but not dormancy in PHYA overexpressors and wild-type of hybrid aspen. *Plant, Cell & Environment*, 28(12), 1579-1588.
- R Development Core Team (2019) R: A Language and Environment for Statistical computing. https://www.r-project.org/
- Rageau, R. (1982). Etude expérimentale des lois d'action de la température sur la croissance des bourgeons floraux du pêcher (*Prunus* persica L. Batsch) pendant la postdormance.
- Réaumur, R. A. F. d. 1735. Observations du thermomètre, faites à Paris durant l'année 1735, comparées avec celles qui ont été faites sous la ligne, à l'isle de France, à Alger et quelques unes de nos isles de l'Amérique. Mémoires de l'Académie des Sciences de Paris.
- Richardson, E. A., EA, R., SD, S., & DR, W. (1974). A model for estimating the completion of rest for" Redhaven" and" Elberta" peach trees.
- Vegis, A. (1964). Dormancy in higher plants. *Annual review of plant physiology*, 15(1), 185-224.

- Vitasse, Y., Signarbieux, C., & Fu, Y. H. (2018). Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences*, *115*(5), 1004-1008.
- Weinberger, J. H. (1950). Chilling requirements of peach varieties. In *Proceedings. American Society for Horticultural Science* (Vol. 56, pp. 122-8).
- Weinberger, J. H. (1956). Prolonged dormancy trouble in peaches in the southeast in relation to winter temperatures. Journal of the American Society for Horticultural Science, 67, 107-112.
- Weinberger, J. H. (1967). Some temperature relations in natural breaking of the rest of Peach flower buds in the San Joaquin Valley, California. Proceedings of the American Society for Horticultural Science, 51, 84-89.
- Welling, A., Kaikuranta, P., & Rinne, P. (1997). Photoperiodic induction of dormancy and freezing tolerance in Betula pubescens. Involvement of ABA and dehydrins. *Physiologia Plantarum*, *100*(1), 119-125.
- Welling, A., Moritz, T., Palva, E. T., & Junttila, O. (2002). Independent activation of cold acclimation by low temperature and short photoperiod in hybrid aspen. *Plant Physiology*, *129*(4), 1633-1641.

Acknowledgements

The author wants to acknowledge the essential contribution of Marc Bonhomme, Aline Faure, Jean-Claude Mauget, Remi Rageau, Jean-Pierre Richard for dormancy release date measurements. Phenological data and stem materials were provided by Neus Aleita, Romain Baffoin, Fabrice Lheureux, Marianne Naudin and Eloise Tranchand. The author is also thankful to Thierry Améglio, André Lacointe and Heikki Hänninen for constructive comments on preliminary versions of the manuscript. Part of the collected data were supported by the Pôle National de Données de la Biodiversité (a.k.a SOERE Tempo) and by a 'Pari Scientifique' grant from the division Agroecosystem of INRAE.

Figure captions

 Table 1 Site and dataset descriptions.

Table 2. Quality of the prediction of endodormancy release dates (ER) using different functions and two different calibration datasets. RMSE, RMSEP and AIC lower than 110% of the minimum RMSE or RMSEP are indicated in bold. Dates for onset of chilling accumulation (D_{CA}) were either fixed (Julian Day) 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). Ori and adj refer to the original published version (ori) or adjusted to the data (adj). Chilling effect were only positive, using the reverse Richardson function, or positive at low temperature and negative at warm temperature, using the smoothed Utah function.

Table 3. Quality of the prediction of budburst dates (BB) using different functions and two different calibration datasets. RMSE, RMSEP and AIC lower than 110% of the minimum RMSE or RMSEP are indicated in bold. Dates for onset of chilling accumulation (D_{CA}) were either fixed (Julian Day) 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 DORMPHOT (DP). Ori and Adj refer to the original published version (ori) or adjusted to the data (adj). Chilling effect were only positive or positive at low temperature and negative at warm temperature, using the reverse Richardson and smoothed Utah functions respectively.

Figure 1. A. Time to break buds under forcing conditions for one node cuttings of Juglans regia cv Franquette. Different colors represent the different phenological stages based on the dynamics in time to break buds. **B-D.** Correlations between the onset of endodormancy induction, the maximum endodormancy depth and endodormancy release.

Figure 2. Average dates of onset of chilling accumulation (A), endodormancy release (B) and budburst (C) predicted across France under current climatic conditions.

Figure 3. A-C. Average date of onset of chilling accumulation (A), endodormancy release (B) and budburst (C) depending on mean annual temperature across France under different climatic *scenarii*. Exponential (A, B) and cubic (C) functions were represented in black dashed lines.

Figure 4 A-C Distribution of the mean (A-C) and variance (D-E) in the date of onset of chilling accumulation (A, D), endodormancy release (B, E) and budburst (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. **G-I** Distribution of the variation compared to the reference period in the mean date of onset of chilling accumulation (G), endodormancy release (H) and budburst (I). The box represents 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. Different letters indicate a significantly different distribution across scenario according to the non-parametric Kruskal Wallis test.

Figure 5. Relative change compared to the present period in average budburst dates across France according to different climatic *scenarii* (RCP2.6, RCP4.5 and RCP 8.5)

and time periods (2006-2050 and 2051-2100). Earlier and later budburst dates than the current climate are represented in blue and red, respectively.

Supplementary material

Table S1. Formalisms used to define the onset of chilling accumulation (DCA) across various studies aiming at modeling phenology in various species and location: fixed or flexible date. Chilling models are sigmoid (Hanninen, 1990), normal (Chuine, 2000; Chuine et al., 2003), Utah (Richardson et al., 1974) and variations (smoothed Utah: Bonhomme et al., 2010, Positive Utah and positive Chill Unit for low chilling varieties: Gilreath and Buchanan, 1981), Dynamic (Fishman et al., 1987a,b), Chilling Hours (Weinberger; 1967), Bidabé (Bidabé, 1965a, b), Growing Degree Day (Ritchie and NeSmith, 1991). NH and SH mean northern and southern hemisphere, respectively.

Figure S1. Average dates of onset of chilling accumulation predicted across France under future climatic *scenarii* (**A**, **D** RCP 2.6; **B**, **E** RCP 4.5 and **C**, **F** RP 8.5). The higher and lower maps represent the short term (**A-C** 2006-2050) and the long term period (**D-F** 2050-2100), respectively.

Figure S2. Average dates of endodormancy release predicted across France under future climatic *scenarii* (**A**, **D** RCP 2.6; **B**, **E** RCP 4.5 and **C**, **F** RP 8.5). The higher and lower maps represent the short term (**A-C** 2006-2050) and the long term period (**D-F** 2050-2100), respectively.

Figure S3. Average dates of budburst predicted across France under future climatic *scenarii* (**A**, **D** RCP 2.6; **B**, **E** RCP 4.5 and **C**, **F** RP 8.5). The higher and lower maps represent the short term (**A-C** 2006-2050) and the long term period (**D-F** 2050-2100), respectively.

Table 1. Site and dataset descriptions

Location	Elevation	Latitude	Longitude	Mean	Minimum	Absolute	Number	First	Last		Number of ol	oservations	
	(m asl.)	o	٥	annuai temperature	temperature (°C)	temperature (°C)	freezing events	Frost (Autumn)	Frost (Spring)	Endodormancy Release		Budburst	
				(°C)				DOY	DOY	Dataset 1	Dataset 2	Dataset 1	Dataset 2
										(C/V)	(C/V)	(C/V)	(C/V)
Balandran	69	43.758	4.516	16.90	12.00	-3.78	14.5	340	50	1/1	1/1	0/0	0/0
Chatte	304	45.143	5.282	13.62	8.15	-9.39	61.7	308	102	0/0	0/0	12/11	11/12
Creysse	115	44.887	1.597	14.65	8.52	-8.50	52.4	309	104	0/0	0/0	13/12	12/13
Crouël	340	45.779	3.142	13.25	9.26	-11.51	59.6	302	108	13/12	12/13	4/4	4/4
Orcival	1150	45.683	2.842	12.92	7.72	-12.13	97.4	291	126	1/1	1/1	1/0	0/1
Terrasson	90	45.136	1.300	14.61	8.96	-9.69	47.4	311	100	1/1	1/1	1/0	0/1
Theix	945	45.706	3.021	9.70	6.22	-15.11	100.3	282	129	1/1	1/1	1/0	0/1
Toulenne	22	44.557	-0.263	15.38	10.56	-6.09	25.9	325	74	1/0	0/1	9/9	9/9

Table 2. Quality of the prediction of endodormancy release dates (ER) using different 2functions and two different calibration datasets. RMSE, RMSEP and AIC lower than 110% of 3the minimum RMSE or RMSEP are indicated in bold. Dates for onset of chilling accumulation 4(D_{CA}) were either fixed (Julian Day) or computed according to: date of first frost (FF), minimum 5temperature (T_{min}), mean temperature (T_{mean}), photoperiod, minimum chilling unit (CU_{min}), leaf 6fall using temperature (LFT) or temperature and photoperiod (LFPT) and dormancy induction 7state using the DORMPHOT model (DP). Ori and adj refer to the original published version 8(ori) or adjusted to the data (adj). Chilling effect were only positive, using the reverse 9Richardson function, or positive at low temperature and negative at warm temperature, using 10the smoothed Utah function.

Onset of chilling	Chilling effect			Dataset 1					Datase	t 2
accumulation D _{CA}			n	RMSE	RMSEP	AIC	n	RMSE	RMSEP	AIC
Julian Day	Positive only	4	18	12.16	11.57	97.9	17	8.96	13.58	82.6
Julian Day	Positive & negative	6	18	12.50	11.49	102.9	17	9.51	14.26	88.6
Moon Tomp	Positive only	4	18	12.63	11.18	99.3	17	9.36	13.46	84.0
mean remp	Positive & negative	6	18	13.24	11.00	105.0	17	10.39	19.22	91.6
Min Tomp	Positive only	4	18	12.64	10.47	99.3	17	9.53	13.50	84.7
wiin remp	Positive & negative	6	18	12.92	9.32	104.1	17	9.40	14.31	88.2
Eirot Eroot	Positive only	3	18	17.12	13.30	108.3	17	13.28	17.76	93.9
FIIST FIOST	Positive & negative	5	18	14.78	12.58	106.9	17	11.22	15.58	92.2
Destoporied	Positive only	4	18	12.31	10.31	98.4	17	7.80	13.90	77.8
	Positive & negative	6	18	14.39	12.85	108.0	17	8.57	14.31	85.0
	Positive only	3	18	15.02	12.82	103.5	17	11.23	16.21	88.2
	Positive & negative	1	18	44.35	47.87	138.5	17	51.32	40.07	135.9
	Positive only	7	18	12.77	10.56	105.7	17	10.28	13.36	93.2
	Positive & negative	9	18	13.27	8.30	111.1	17	8.68	13.48	91.5
Loof Foll Thormolori	Positive only	3	18	12.88	10.30	98.0	17	9.21	13.98	81.5
Lear Fair Thermar on	Positive & negative	5	18	12.83	10.12	101.9	17	9.11	14.19	85.1
Loof Foll Thormal adj	Positive only	6	18	11.91	10.77	101.2	17	7.79	13.59	81.8
Lear Fair Mennarauj	Positive & negative	8	18	11.86	13.29	105.0	17	7.75	14.43	85.6
Loof Fall Photothormal ari	Positive only	3	18	13.23	8.54	99.0	17	8.08	13.98	77.0
	Positive & negative	5	18	13.42	8.99	103.5	17	7.71	14.24	79.4
Loof Fall Photothormal adj	Positive only	6	18	12.73	8.72	103.6	17	7.86	14.15	82.1
	Positive & negative	8	18	12.26	10.67	106.2	17	7.64	14.06	85.1
	Positive only	3	18	12.77	9.08	97.7	17	8.20	13.86	77.5
	Positive & negative	5	18	13.11	9.55	102.6	17	8.87	14.38	84.2
	Positive only	7	18	11.79	8.45	102.8	17	7.72	12.90	83.5
	Positive & negative	9	18	11.51	10.35	105.9	17	7.20	14.27	85.1

13**Table 3.** Quality of the prediction of budburst dates (BB) using different functions and two 14different calibration datasets. RMSE, RMSEP and AIC lower than 110% of the minimum 15RMSE or RMSEP are indicated in bold. Dates for onset of chilling accumulation (D_{CA}) were 16either fixed (Julian Day) or computed according to date of first frost (FF), minimum 17temperature (T_{min}), mean temperature (T_{mean}), photoperiod, minimum chilling unit (CU_{min}), 18Leaf fall using temperature (LFT) or temperature and photoperiod (LFPT) and DORMPHOT 19(DP). Ori and Adj refer to the original published version (ori) or adjusted to the data (adj). 20Chilling effect were only positive or positive at low temperature and negative at warm 21temperature, using the reverse Richardson and smoothed Utah functions respectively.

Onset of chilling	Chilling effect			Data	aset 1	Dataset	et 2			
accumulation D _{CA}			n	RMSE	RMSEP	AIC	n	RMSE	RMSEP	AIC
Julian Day	Positive only	5	41	8.04	7.06	180.9	39	6.92	7.27	160.9
Julian Day	Positive & negative	7	41	8.15	7.25	186.1	39	7.28	7.88	168.8
Moon Tomp	Positive only	5	41	8.10	7.31	181.5	39	7.69	7.55	169.1
Mean Temp	Positive & negative	7	41	8.63	7.86	190.7	39	8.86	7.89	184.1
Min Tomp	Positive only	5	41	7.85	7.21	178.9	39	7.58	7.57	168.0
	Positive & negative	7	41	11.36	12.73	213.3	39	10.97	10.00	200.9
First Frost	Positive only	4	41	9.52	16.29	192.7	39	14.72	8.75	217.7
FIISEFIOSE	Positive & negative	6	41	40.95	86.24	316.4	39	72.30	10.69	345.9
Destoporied	Positive only	5	41	8.01	6.74	180.7	39	6.94	7.32	161.1
Filotoperiod	Positive & negative	7	41	9.66	7.97	199.9	39	7.18	8.09	167.8
	Positive only	4	41	11.17	10.88	205.9	39	9.33	9.27	182.2
	Positive & negative	2	41	54.34	63.04	331.6	39	63.84	55.42	328.2
	Positive only	8	41	7.94	7.48	185.9	39	7.81	7.66	176.3
	Positive & negative	10	41	9.80	9.75	207.1	39	10.29	10.56	201.8
Loof Foll Thormol ori	Positive only	4	41	7.67	6.88	175.0	39	7.66	7.70	166.8
	Positive & negative	6	41	7.75	6.76	179.9	39	7.36	7.41	167.7
Loof Fall Thormal adi	Positive only	7	41	8.30	6.77	187.6	39	6.84	7.29	163.9
Lear Fair Mennarauj	Positive & negative	9	41	8.31	7.71	191.6	39	6.92	7.42	168.9
Loof Fall Photothormal ari	Positive only	4	41	7.82	7.16	176.6	39	7.08	7.37	160.7
	Positive & negative	6	41	7.47	6.68	176.9	39	7.01	7.18	163.9
Loof Fall Photothormal adi	Positive only	7	41	7.49	6.82	179.1	39	6.97	7.23	165.4
	Positive & negative	9	41	80.49	73.53	377.8	39	7.14	6.94	171.3
	Positive only	4	41	7.74	6.89	175.9	39	7.13	7.63	161.3
	Positive & negative	6	41	7.39	6.82	176.0	39	7.05	7.51	164.4
	Positive only	8	41	7.67	6.90	183.1	39	7.28	7.67	170.9
	Positive & negative	10	41	8.88	7.04	199.1	39	7.00	8.23	171.8

22

23



Figure 1. A. Time to break buds under forcing conditions for one node cuttings of Juglans 27regia cv Franquette. Different colors represent the different phenological stages based on 28the dynamics in time to break buds. **B-D.** Correlations between the onset of endodormancy 29induction, the maximum endodormancy depth and endodormancy release.



Figure 2. Average dates of onset of chilling accumulation (A), endodormancy release (B) 33and budburst (C) predicted across France under current climatic conditions.



Figure 3. A-C. Average date of onset of chilling accumulation (A), endodormancy release 38(B) and budburst (C) depending on mean annual temperature across France under different 39climatic *scenarii*. Exponential (A, B) and cubic (C) functions were represented in black 40dashed lines.



Figure 4 A-C Distribution of the mean (A-C) and variance (D-E) in the date of onset of 44chilling accumulation (A, D), endodormancy release (B, E) and budburst (C, F) in the 45current period (Ref) or RCP scenario in the early (2006-2050) and late part of the XXI 46century (2051-2100) in France. **G-I** Distribution of the variation compared to the reference 47period in the mean date of onset of chilling accumulation (G), endodormancy release (H) 48and budburst (I). The box represents the upper and lower quartile with the median indicated 49by a thick black line, the whiskers represents the 1st and 9th decile, outliers were not 50 represented. Different letters indicate a significantly different distribution across scenario 51 according to the non-parametric Kruskal Wallis test.



Figure 5. Relative change compared to the present period in average budburst dates 54across France according to different climatic *scenarii* (RCP2.6, RCP4.5 and RCP 8.5) and 55time periods (2006-2050 and 2051-2100). Earlier and later budburst dates than the current 56climate are represented in blue and red, respectively.