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# **Starting the winter season: predicting endodormancy induction through multi-process modeling.**

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## 1 **Abstract**

2 In perennial plants, the annual phenological cycle is subdivided into successive stages whose  
3 completion will lead directly to the onset of the following one. A critical point is the transition  
4 between the apparent vegetative growth and the cryptic dormancy. To date, the initial date for  
5 chilling accumulation ( $D_{CA}$ ) is arbitrarily set using various rules such as fixed or dynamic dates  
6 depending on environmental variables. These rules led to tremendous variability across studies  
7 and sites (from late summer until late autumn). To test the relevancy of different  $D_{CA}$ , we used  
8 a dataset combining dormancy release dates, budburst dates and frost hardiness measurements  
9 from 50 years in various orchards across France and Spain for *J. regia* cv Franquette. Many of  
10 the tested  $D_{CA}$  provided accurate results for the calibration and validation datasets ( $RMSEP <$   
11  $10$  and  $8$  days for endodormancy release and budburst dates, respectively). However, for frost  
12 hardiness, only the  $D_{CA}$  provided by the DORMPHOT model provided accurate results  
13 ( $RMSEP < 3^{\circ}C$ ). The best  $D_{CA}$  was thus selected using a composite index for all three processes.  
14 Testing the prediction under current and future climatic scenario showed that in, up to 25% of  
15 French territory under RCP 8.5 scenario, ecodormancy stage is likely to be delayed although  
16 temperature is decreasing. Overall, less average frost damages are expected although decennial  
17 risk (*i.e.* return period of ten years) is likely to increase in autumn in 15% of French territory.  
18 In southern part of France, delayed dormancy induction and release would induce delayed  
19 budburst and blooming altering flower and fruit production, whereas North East and Massif  
20 Central parts of France may suffer higher frost risks from late frost acclimation. Finally, this  
21 study describes relationships between climatic variables and plant phenological processes to  
22 build metamodels predicting next century's phenological cycles at the global scale.

23

24 **Keywords:** Chilling, Frost acclimation, Frost damages, Forcing, Photoperiod, Phenology, Risk  
25 assessment, Tree.

## 26 **Introduction**

27 In frost-exposed environments, deciduous trees have to timely adjust their biology and  
28 increase frost resistance by anticipating unfavorable conditions before the winter period. As  
29 observed for most stresses, avoidance and tolerance are two complementary processes driving  
30 frost resistance (Charrier *et al.*, 2011). The protection of shoot apical meristems under bud  
31 scales can be considered as an avoidance strategy. This is achieved through physiological  
32 changes allowing the transition from an apparently active (*e.g.* primary and secondary growth,  
33 leaf expansion, fruit maturation) towards a ‘dormant’ period (*e.g.* endodormancy and  
34 ecodormancy; Lang *et al.*, 1987). During this transition, different phenologically-related  
35 processes that are either visible (*e.g.* leaf fall, growth cessation, lignification or budset) or  
36 invisible (*e.g.* dormancy induction and release) take place. In parallel, trees transiently increase  
37 their frost tolerance through frost acclimation / deacclimation process (Charrier *et al.*, 2011).

38 In autumn, endodormancy release and frost acclimation are induced by the same  
39 environmental factors, namely decreasing temperature and photoperiod (Welling *et al.*, 2002;  
40 Arora *et al.*, 2003; Maurya & Bahlerao, 2017). After endodormancy was released, ecodormancy  
41 and frost deacclimation also occurs in parallel, under the control of warm temperature, in most  
42 species, eventually modulated by photoperiod in photosensitive species, such as late  
43 successional species (Basler & Körner, 2012). Process-based models using these variables as  
44 input have been developed to simulate the dormancy release and budburst dates (Chuine *et al.*,  
45 2016), as well as frost hardiness (*e.g.* Leinonen 1996; Ferguson *et al.*, 2011; Charrier *et al.*,  
46 2018).

47 Under the context of global change, it is particularly critical to accurately predict future  
48 trends in warmer climates. Since the first empirical model describing the relation between  
49 temperature and plant development, through the thermal-time concept (Réaumur, 1735),  
50 budburst and blooming models were only computing accumulation of growth-effective

51 temperature *i.e.* growth degree days (GDD). As the starting point was set at the coldest period  
52 of the year (*i.e.* January 1<sup>st</sup> or July 1<sup>st</sup> in northern and southern hemisphere, respectively), these  
53 models provided accurate results. However, this type of model was not efficient under warmer  
54 winter areas, where temperate crop species were attempted to grow (*e.g.* Northern Africa,  
55 Middle East or South America; Balandier *et al.*, 1993). In this context, temperate perennial  
56 crops did exhibit lack of chilling and insufficient endodormancy release (Weinberger, 1950).  
57 The process of endodormancy, and related chilling accumulation, had thus been introduced into  
58 models (Weinberger, 1956; Vegis 1964). In the recent decades, naturally growing trees have  
59 also been affected by a reduction in chilling exposure throughout winter, enhancing the interest  
60 into the endodormancy stage (Gauzere *et al.*, 2019).

61 Two-step models, simulating endo- and ecodormancy stages, are now commonly used to  
62 predict budburst dates (Chuine *et al.*, 2016). Frost acclimation models use similar formalism  
63 with direct linkage between frost acclimation and exposure to chilling temperatures followed  
64 by frost deacclimation and exposure to forcing temperatures, respectively. In perennial plants,  
65 the completion of a stage will directly drive the onset of the following ones (Hänninen &  
66 Tanino, 2011). However, the initial date for chilling accumulation ( $D_{CA}$ ) is usually arbitrarily  
67 set with various rules leading to tremendous variability across studies (from late summer until  
68 late autumn). Four different concepts of  $D_{CA}$  have been used (see Tab. S1):

- 69 - Fixed date across years and locations: from September 1<sup>st</sup> (Chuine *et al.*, 2016) until  
70 November 1<sup>st</sup> (Weinberger, 1967), for northern hemisphere,
- 71 - Dynamic date through a simple climatic threshold: critical temperature (*e.g.* date of the first  
72 frost; Landsberg, 1974) or photoperiod (Welling *et al.*, 1997),
- 73 - Dynamic date through a mathematic function using a single variable such as the date of  
74 minimum chilling units computed by the Utah model (Richardson *et al.*, 1974),

75 - Dynamic date through a mathematic function using interacting variables (temperature and  
76 photoperiod) simulating leaf fall date (Delpierre *et al.*, 2009) or dormancy induction  
77 (DORMPHOT; Caffarra *et al.*, 2011a).

78 These different approaches have mainly been used for phenological cycle prediction. Thanks  
79 to a large dataset combining data from 50 years in various orchards across France and Spain for  
80 *J. regia* cv Franquette, we tested different formalism to compute the effects of the onset of  
81 chilling accumulation  $D_{CA}$  on the accuracy of three related processes (endodormancy,  
82 ecodormancy and frost acclimation/deacclimation). The optimal model was subsequently  
83 assessed for future climate prediction over France following three contrasted *scenarii*.

## 84 **Material and methods**

### 85 *Endodormancy release and budburst dates*

86 Endodormancy release dates were measured using the one-node-cutting ‘forcing’ test of  
87 Rageau (1982). Samplings were performed every three weeks from October until May and 48  
88 one-node cuttings prepared per sampling date. Buds were isolated from other parts of plant to  
89 prevent correlative inhibitions (Dennis, 2003). At each sampling date, one-year-old stems were  
90 cut in 7-cm long pieces, bearing only one node at the top or less than 1 cm below the top end,  
91 for terminal and axillary buds, respectively. For axillary buds, the top of the cutting was covered  
92 by paraffin wax to prevent desiccation. The bases of the cuttings were immersed into tap water,  
93 weekly changed. Cuttings were exposed to optimal conditions for growth resumption (*i.e.* 16/8  
94 D/N and 25°C) and individually observed every 3 days. Mean time until budburst (stage 09  
95 BBCH) were computed from individual time until budburst for each cutting. After  
96 endodormancy release, buds of *J. regia* cv Franquette break out after 20 days under optimal  
97 conditions (Mauget, 1980; Charrier *et al.*, 2011). Endodormancy release dates were thus  
98 obtained by linear interpolation between the two dates giving a time to budburst higher (or equal

99 to) and lower (or equal to) than 20 days, respectively. Budburst in the field was monitored every  
100 two to three days in the different sites until 50% of buds reached the stage 09 of the BBCH  
101 scale.

### 102 *Frost hardiness*

103 Frost hardiness was measured from September until budburst on one-year-old branches in  
104 different orchards (Tab. 1) using the electrolyte leakage method (Charrier & Améglio 2011).  
105 Samples were cut into six 7-cm-long segments without buds and exposed to four different  
106 freezing temperatures among this set of temperatures: -5, -10, -15, -20, -30 and -40 °C.  
107 Depending on the season, either the highest or the lowest temperatures were not used. Two  
108 supplementary subsamples were exposed to control (+5 °C) and maximal freezing temperature  
109 (-80 °C). Freezing and thawing rates were set to 5 K h<sup>-1</sup>.

110 Relative electrolytic leakage (REL) was calculated as (C1/C2) as described in Zhang &  
111 Willison (1987). We assumed a sigmoidal relationship between REL and temperature ( $\theta$ ) for  
112 each sample:

$$113 \quad REL = \frac{a}{1+e^{b(c-\theta)}} + d \quad (1)$$

114 where parameters a and d define asymptotes of the function, and b is the slope at the inflection  
115 point c.

116 Frost hardiness was defined as the temperature of the inflection point (c) of the adjusted logistic  
117 sigmoid function (Repo & Lappi 1989), whereas frost sensitivity was considered to be estimated  
118 by the parameter b in percent damage per Celsius degree.

### 119 *Climate data*

120 Models were fit using observed daily mean and minimal temperature monitored by weather  
121 station, located most of the time in the same orchard and closer than 10km distance (Table 1).

122 For predictive purpose, the temperature, calculated according to the CNRM-ALADIN52 model  
123 and corrected by a Q-Q method (Déqué *et al.*, 2007), were used from 8462 sites across France  
124 (Safran grid at 8km spatial resolution; MétéoFrance). Four datasets were used as input variable:  
125 reference period (1950-2005) and three contrasted climatic *scenarii* (RCP 2.6, RCP 4.5 and  
126 RCP 8.5) for the future period (2005-2100). For each site and day, day and night length were  
127 computed depending on the latitude and day of year.

### 128 *Endodormancy induction and onset of chilling accumulation*

129 Date of the onset of chilling accumulation ( $D_{CA}$ ) was computed through different functions:

130 i) Fixed  $D_{CA}$  every *ca.* 10 days from DOY 182 (July 1<sup>st</sup>) until DOY 335 (November 30<sup>th</sup>).

131 ii) Dynamic  $D_{CA}$  based on threshold values reached by minimum temperature ( $T_{min}$ ), mean  
132 temperature ( $T_{mean}$ ), first frost (FF) or photoperiod.

133 iii) Date of minimum chilling units ( $CU_{min}$ ) were computed according to the Utah model  
134 (originally developed on *Prunus persica*) that computes negative chilling effect for  
135 temperature higher than 16°C (Richardson *et al.*, 1974). Daily CU started were summed  
136 from DOY 182 (July 1<sup>st</sup>) until DOY 365 (December 31<sup>st</sup>) using the Utah\_Model function  
137 (ChillR package; Luedeling, 2019).

138 iv) Predicted leaf fall dates (BBCH 97) were computed according to the thermal (LFT) and  
139 photothermal (LFPT) models developed by Delpierre *et al.* (2009) and developed in *Quercus*  
140 and *Quercus + Fagus*, respectively. Below a critical photoperiod, temperature colder than a  
141 threshold, modulated by a photoperiod function in the case of the LFPT model, are summed  
142 up to a critical value ( $Y_{crit}$ ), corresponding to the leaf fall date. Both LFT and LFPT model  
143 were computed using the original or a modified set of parameters:  $LF(P)T_{ori}$  and  $LF(P)T_{mod}$ ,  
144 respectively.

145 v) The dormancy induction state (DS) was computed according to the DORMPHOT model  
146 developed in *Betula pubescens* by Caffarra *et al.* (2011a). The two sigmoidal response



147 function to low temperature and photoperiod, respectively interact through sigmoidal  
148 functions. The original ( $DP_{ori}$ ) and two modified ( $DP_E$  and  $DP_L$ , for early and late,  
149 respectively) sets of parameters were used.

#### 150 *Endodormancy release and budburst*

151 Starting from  $D_{CA}$ , the sum of CU was modeled according to the inverse of the Richardson  
152 function (Richardson *et al.*, 1974) which was defined as the best function predicting  
153 endodormancy release dates in walnut trees (Chuine *et al.*, 2016; Charrier *et al.*, 2018).  
154 According to the sequential paradigm, the date where  $CU(t)$  reaches the critical threshold  $CU_{crit}$   
155 (arbitrary chilling units,  $CU$ ) is the date of endodormancy release ( $D_{ER}$ ), or the transition  
156 between endodormancy and ecodormancy!

$$157 \quad CU(t + 1) = CU(t) + Max(\text{Min}(T_{high} - \theta(t); T_{high} - T_{low}); 0) \quad (2)$$

158 with  $CU(t)$ , the chilling unit at day  $t$ ,  $T_{high}$ , both the temperature above which CU equals 0 and  
159 the amount of CU when temperature equals  $T_{low}$  or lower; CU being linear between  $T_{low}$  and  
160  $T_{high}$ .

161 The ontogenetic development during ecodormancy stage was modeled according to a  
162 sigmoid function (Caffarra *et al.*, 2011a). The date when  $FU(t)$  reaches the critical threshold  
163  $FU_{crit}$  (arbitrary forcing units,  $FU$ ) is the budburst date ( $D_{BB}$ ).

$$164 \quad FU(t + 1) = FU(t) + \frac{1}{1 + e^{-slp(\theta(t) - T_{50})}} \quad (3)$$

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

#### 167 *Frost hardiness and frost damages*

168 Frost hardiness and subsequent frost damages were computed using a photothermal model  
169 developed on *Pinus sylvestris* (Leinonen, 1996) and adapted on *Juglans regia* (Charrier *et al.*,

2018). Shortly, hardening ability ( $C_R$ ) changes in relation to the different stage of the annual cycle (endodormancy induction, endodormancy release, ecodormancy and growth). During endodormancy and growth stages,  $C_R$  was set to 1 and 0, respectively. During endodormancy induction,  $C_R$  was either considered gradually increasing from 0 to 1 during the 30 days before the onset of chilling accumulation (Fixed  $D_{CA}$ ). For simple dynamic  $D_{CA}$ ,  $C_R$  was set to 0 until the threshold was reached ( $CU_{min}$ , FF,  $T_{min}$ ,  $T_{mean}$  or Photoperiod). For models describing continuous process,  $C_R$  was defined as the ratio between the related variable and its critical threshold (LF, LFPT and DP models). From the interaction between hardening, temperature and photoperiod, a dynamic potential state of hardiness is computed throughout the year. Daily changes in actual frost hardiness (FH) tend to reduce the difference between potential state of hardiness and FH with a temporal lag (see complete description of the model in the original publication). Frost damages are computed on a daily basis through the relation between FH, frost sensitivity (FS, slope at FH) and minimum temperature  $\theta_{min}$  as:

$$FD = \frac{1}{1 + e^{FS(FH - \theta_{min})}} \quad (4)$$

#### 184 *Model calibration depending on the onset of chilling accumulation*

185 Three different sub-models, namely endodormancy release, ecodormancy release and frost  
186 hardiness, were calibrated one after the other, as they were interrelated. To minimize sums of  
187 square between observed and predicted values, we used the nls function (Gauss-Newton  
188 algorithm), with different sets of starting values at minimum, average and maximum ranges of  
189 parameter realistic values.

190 For endodormancy release model, one parameter was optimized:  $CU_{crit}$  corresponding to the  
191 sum of chilling units to release endodormancy. The other parameters were set to the values  
192 defined by Chuine *et al.* (2016). The dataset was split into calibration and validation datasets

193 containing 18 observations from 6 sites and 16 observations from 5 sites, respectively (Table  
 194 1).

195 For ecodormancy model, one parameter was optimized:  $FU_{crit}$  corresponding to the sum of  
 196 forcing units to break buds. The endodormancy model used to predict  $D_{ER}$  was the best from  
 197 the previous step and the other parameters set to the values described in Charrier *et al.* (2018).  
 198 The dataset was split into calibration and validation datasets containing 41 observations from 7  
 199 sites and 36 observations from 4 sites, respectively (Table 1).

200 For frost hardiness model, seven parameters were optimized:  $T_1$ ,  $T_2$ ,  $NL_1$ ,  $NL_2$ ,  $\delta$ ,  $\tau$  and  
 201  $FU_{critR}$ . The endodormancy and ecodormancy models used to predict  $D_{ER}$  and  $D_{BB}$ , were the  
 202 best from the previous steps and the other parameters set to the values described in Charrier *et*  
 203 *al.* (2018). The dataset was split into calibration and validation datasets containing 60  
 204 observations (6 winter periods) from 2 sites and 51 observations (5 winter periods) from 5 sites,  
 205 respectively (Table 1).

206 The quality of the fit and the predictive ability of the models depending on  $D_{CA}$  were assessed  
 207 for calibration and validation datasets computing Root Mean Square Error (RMSE) and  
 208 Predictive Root Mean Square Error (RMSEP), respectively:

$$209 \quad RMSE(P) = \sqrt{\frac{\sum_{i=1}^n (\hat{y}_i - y_i)^2}{n}} \quad (5)$$

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

211 As the different  $D_{CA}$  provided contrasted results among models, we used a composite  
 212 performance index defined as :

$$213 \quad PI = \frac{RMSE_{endoD_i}}{\max(RMSE_{endoD})} + \frac{RMSE_{ecoD_i}}{\max(RMSE_{ecoD})} + \frac{RMSE_{FH_i}}{\max(RMSEP_{FH})} + \frac{RMSEP_{endoD_i}}{\max(RMSEP_{endoD})} +$$

$$214 \quad \frac{RMSEP_{ecoD_i}}{\max(RMSEP_{ecoD})} + \frac{RMSEP_{FH_i}}{\max(RMSEP_{FH})} \quad (6)$$

## 215 **Results**

### 216 *Effects of $D_{CA}$ on model accuracy*

217 Fixed  $D_{CA}$  only had a relatively small effect on the quality of the fit ( $12.3 < RMSE_{endoD} <$   
218  $15.1$  days; coefficient of variation  $CV = 6.8\%$  for a 153 days range) and the predictive ability  
219 of  $D_{ER}$  ( $8.3 < RMSEP_{endoD} < 11.8$  days;  $CV = 11.7\%$ ). Fixed  $D_{CA}$  between DOY 223 (Aug. 11<sup>th</sup>)  
220 and 274 (Oct. 1<sup>st</sup>) are relatively efficient to simulate CU accumulation with respect to  $D_{ER}$ . The  
221 effect of various  $D_{CA}$  on the prediction of  $D_{BB}$  was also relatively low for the quality of the fit  
222 ( $7.1 < RMSE_{ecoD} < 8.6$  day;  $CV = 6.1\%$ ) and the predictive ability ( $6.9 < RMSEP_{ecoD} < 8.1$   
223 days;  $CV = 4.7\%$ ). A wider range of fixed  $D_{CA}$ , *i.e.* between 223 and 325 (Nov. 21<sup>st</sup>), similarly  
224 performed for  $D_{BB}$  prediction. Annual phenological cycle ( $D_{ER}$  and  $D_{BB}$ ) was thus best predicted  
225 when  $D_{CA}$  was set to DOY 254 (*i.e.* Sep. 11<sup>th</sup>). For frost hardiness, fixed  $D_{CA}$  earlier than DOY  
226 305 (Nov. 1<sup>st</sup>) provided highly efficient fit ( $RMSE < 2.0^{\circ}C$ ). However, the prediction was not  
227 accurate enough, as  $RMSEP$  was almost twice higher ( $3.2 < RMSEP < 3.9^{\circ}C$ ).

228 The  $D_{CA}$  returned by the various dynamic functions were highly different across France:  
229 from DOY  $182 \pm 5$  to  $312 \pm 14$  (median  $\pm$  SD; Fig. 1A). Four groups of earliness can be defined:  
230 very early ( $T_{min}$  and photoperiod), early ( $DP_E$ ,  $LFPT_{mod}$ , and  $LFT_{mod}$ ), intermediate ( $CU_{min}$ ) and  
231 late ( $LFT_{ori}$ ,  $LFPT_{ori}$ ,  $DP_{ori}$ ,  $DP_L$  and  $FF$ ). All the dynamic  $D_{CA}$  computed via different functions  
232 exhibited highly significant correlation with mean annual temperature of the site (Fig. 1B-D).

233 Simple temperature thresholds, such as  $T_{min}$  or  $T_{mean}$  did not provide accurate phenological  
234 ( $RMSEP > 11.5$  and  $8.0$  days for  $D_{ER}$  and  $D_{BB}$ , respectively) nor FH prediction ( $RMSEP >$   
235  $3.3^{\circ}C$ ; Tab. 1). The  $D_{CA}$  calculated via a photoperiodic threshold was relatively efficient to  
236 predict  $D_{BB}$  ( $RMSEP = 6.8$  days), but not  $D_{ER}$  ( $RMSEP = 10.2$  days) nor FH ( $RMSEP = 3.5^{\circ}C$ ).

237 The  $D_{CA}$  computed using the Utah function did not provide accurate prediction for any  
238 variable of interest ( $RMSEP = 14.1$  days,  $7.8$  days and  $3.5^{\circ}C$  for  $D_{ER}$ ,  $D_{BB}$  and FH,

239 respectively). The leaf fall thermal function (LFT), using either the original (LFT<sub>ori</sub>) or the  
240 modified sets of parameters (LFT<sub>mod</sub>), was relatively efficient to predict D<sub>BB</sub> (RMSEP = 7.23  
241 days) but less efficient for D<sub>ER</sub> and FH (RMSEP ≥ 9.2 and 3.2 for D<sub>ER</sub> and FH, respectively).  
242 The leaf fall photothermal function (LFPT) provided accurate predictions for phenological  
243 dates (RMSEP ≤ 8.8 and 6.9 days for D<sub>ER</sub> and D<sub>BB</sub> respectively) but not for FH (RMSEP > 3.2  
244 °C). The D<sub>CA</sub> computed using the DORMPHOT function were the most efficient to predict D<sub>ER</sub>,  
245 D<sub>BB</sub> and FH, in the original and ‘Late’ versions of the function (DP<sub>ori</sub>, and DP<sub>L</sub>, respectively).  
246 Finally, the performance index (PI) accounting for all the models and methods of computing  
247 D<sub>CA</sub> could not distinguish between DP<sub>ori</sub> and DP<sub>L</sub> (PI = 6.31).

248 Finally, the different processes exhibited contrasted thickness linkage with D<sub>CA</sub>. For  
249 ecodormancy, a wide range of fixed date (100 days range: Aug. 11<sup>th</sup> until Nov. 21<sup>st</sup>) and all the  
250 computations using photoperiod as an input variable, provided good fit and predictive  
251 accuracies (RMSE<sub>EcoD</sub> and RMSE<sub>EndoD</sub> lower than 8 and 7.6 days, respectively). Endodormancy  
252 release was slightly more restrictive with the best predictions either provided by fixed calendar  
253 dates (Aug. 11<sup>th</sup> until Oct. 1<sup>st</sup>) or dynamic functions integrating the interaction between  
254 temperature and photoperiod (LFPT and DP). Frost hardiness was the most restrictive, with  
255 excellent predictive accuracy when using D<sub>CA</sub> computed by DORMPHOT model (DP<sub>ori</sub> and  
256 DP<sub>L</sub>; RMSEP < 3.0°C) compared to all the other computations.

257 Although both DP<sub>ori</sub> and DP<sub>L</sub> performed almost equally for the three variables of interest  
258 (D<sub>ER</sub>, D<sub>BB</sub> and FH), DP<sub>L</sub> exhibited a slightly better correlation to predict the dynamic of Mean  
259 Time until budburst (MTB) during the period of dormancy induction (R<sup>2</sup> = 0.262 and 0.282 for  
260 DP<sub>ori</sub> and DP<sub>L</sub>, respectively; Figure 2). Furthermore, as FH was slightly better predicted using  
261 DP<sub>L</sub> (RMSEP = 2.6°C), D<sub>CA</sub> predicted by this function was selected to predict the current and  
262 future frost risks (Fig. 3).

263 *Predictions under current and future climates*

264 Using  $D_{CA}$  computed from  $DP_L$  endodormancy release dates under current climate exhibited  
265 a structured geographical pattern across France. Endodormancy release dates spanned over a  
266 60 days range (Fig. 3A): earlier in mountain area (Early December) and later on the  
267 Mediterranean (Mid-February) and southwestern coasts (Late January). Budburst dates  
268 exhibited an opposite pattern over a 77 days range (Fig. 3B): from Mid-April in Southern and  
269 Western parts until late June in mountainous area. Endodormancy release and budburst dates  
270 were highly correlated to mean annual temperature, although through different functions  
271 (exponential and cubic function for endodormancy release and budburst, respectively; Fig. 3C-  
272 D).

273 The geographic structure was less obvious for frost damages, with very low predicted  
274 damages during autumn (Fig. 4A) and spring (Fig. 4C), except in high mountain area. During  
275 the winter period, higher frost damages are predicted in the northeastern part of France  
276 (Burgundy, Alsace, Lorraine), in mountain areas and in the north of Rhone valley (Fig. 4B).  
277 Average predicted damages in autumn and spring were highly correlated to the date of first ( $<-$   
278  $4^{\circ}\text{C}$ ) and last frost event ( $< 0^{\circ}\text{C}$ ), respectively (Fig. 4D; F), whereas maximum winter damages  
279 were correlated to absolute annual temperature (Fig. 4E).

280 Similar trends are observed under future climate predictions, with high delay in both the  
281 onset of dormancy and release for mean annual temperature higher than  $5^{\circ}\text{C}$  (Fig. 5A, B).  
282 However, the delay affecting endodormancy stage does not carry over toward budburst with  
283 earlier budburst with increasing temperature for lower mean annual temperature than  $10^{\circ}\text{C}$  (Fig.  
284 5C). It should be noted that similar or earlier budburst is likely to happen for higher temperature,  
285 and this may be observed in up to one quarter of France at the end of the XXI<sup>st</sup> century: from 5  
286 (RCP 4.5) to 27% (RCP8.5 scenario) of the French territory in 2051-2100 (Fig. 6). Although  
287 such a delay is not forecasted within the 'Noix de Grenoble' Protected Designation of Origin  
288 area, budburst would be delayed in most of the 'Noix du Périgord' area under RCP8.5 scenario

289 (75.1% 2006-2050 and 94.2% 2051-2100). Overall, frost damages are expected to decrease, on  
290 average, all over France (Fig. S1). However, in North East and Massif Central, higher decennial  
291 risks are predicted under RCP 2.6 *scenario* (2006-2051; Fig. S2).

## 292 **Discussion**

293 Defining the initial date for cyclical processes is a critical issue. To predict annual  
294 phenological cycle in perennial organisms, such as trees, various empirical rules have been used  
295 so far. The onset of chilling accumulation during endodormancy stage ( $D_{CA}$ ) had, for instance,  
296 been arbitrarily set using fixed dates across years and locations (Chuine *et al.*, 2016) or, under  
297 the dependence of environmental factors controlling the induction of dormancy (Caffarra *et al.*,  
298 2011b). In the current study, we used long-term observations of phenological stages  
299 (endodormancy release and budburst) and related processes (frost acclimation and  
300 deacclimation) in various environmental conditions and showed that the DORMPHOT model  
301 was the most relevant to predict winter biology in walnut trees.

302 Depending on the studied process, not all computation performed equally (Tab. 2). The  
303 effect of  $D_{CA}$  on ecodormancy and budburst was buffered during endodormancy release. From  
304 a budburst perspective, various rules for  $D_{CA}$  computation can thus be considered as valid,  
305 although they all consider a potential effect of photoperiod, either directly or indirectly via fixed  
306 date (Welling *et al.*, 1997; Chuine and Régnière, 2017). A narrower range of fixed date and  
307 fewer dynamic computations of  $D_{CA}$  (DORMPHOT and LFPT models) provided accurate  
308 predictions for endodormancy release dates. However, providing predictive rules only based on  
309 one or two phenological stages, even though with a large number of measurements (more than  
310 100 dates, combining endodormancy and budburst, in the present study) does not provide  
311 sufficient details for continuous process modeling. Introducing frost hardiness as a co-variable  
312 of dormancy induction and release provided higher temporal resolution into these concurring

313 processes (Welling & Palva, 2006; Charrier *et al.*, 2011; Hanninen, 2016). Through a multi  
314 criterion analysis, the  $D_{CA}$  simulated by the DORMPHOT model provided the most accurate  
315 predictions. This model, originally developed in *Betula pubescens*, is thus relevant for other  
316 deciduous species such as *Juglans regia*. The conceptual development of this model is indeed  
317 based on experimental results combining photoperiod and temperature manipulation (Caffarra  
318 *et al.*, 2011b), whereas other formalisms were based on empirical observations (*e.g.* leaf fall).  
319 Photoperiod and temperature are intimately related in controlling annual weather dynamics.  
320 However, temperature fluctuation is much higher at a given date of the year which could induce  
321 high variability in the onset of the winter season (see *e.g.* Fig.1). Since dormancy induction and  
322 frost acclimation are lengthy processes (*e.g.* ca. 1-2 month), perennial plants cannot only rely  
323 on temperature changes that can be too sudden for the onset of winter rest (Caffarra *et al.*,  
324 2011a). Both photoperiod and temperature variables thus affect annual phenological cycle in  
325 perennial plants, although at different ratio across species. Photoperiod is for instance  
326 predominant in *Populus sp* (Kalcsits *et al.*, 2009) and *Vitis sp* (Fennel & Hoover 1991), while  
327 temperature in *Malus sp* and *Pyrus sp* (Heide & Prestrud, 2005) and *Sorbus sp* (Heide, 2011).  
328 The interaction of both photoperiod and temperature has been showed in *Prunus sp* (Heide  
329 2008). Integrating both variables is an interesting strategy to prevent dormancy induction  
330 during cold late summer (without frost risks) while maintaining physiological activity under  
331 extended warm periods. It has been hypothesized that the modulation of photoperiod sensitivity  
332 by temperature may be related by thermal effect on phytochrome perception of day length  
333 (Mølmann *et al.*, 2005).

334 The selected rule for  $D_{CA}$ , predicting a delayed chilling accumulation in warmer locations  
335 ( $> 7^{\circ}\text{C}$  MAT; Fig. 1C; 5A) would further delay endodormancy release in such area (Fig. 3 A,  
336 C). However, cold weather would limit ontogenetic development during ecodormancy,  
337 providing a negative picture of  $D_{ER}$  vs  $D_{BB}$  (Fig. 3). Under future climatic conditions such as



338 predicted by RCPs *scenarii*, this picture is likely to be blurred as the tipping point for budburst  
339 would be achieved (*ca.* 14°C MAT). Below 14°C, endodormancy would be released and  
340 warmer temperature of the winter-spring period lead to earlier budburst.

341 Date of first frost (< 0°C), minimum temperature and date of late frost (<-4°C) appear as  
342 good proxies to predict early, maximum and late frost damages, respectively (Fig. 4D-F).  
343 Predicted minimal temperature are expected to decrease as well and, even though flushing buds  
344 would be highly vulnerable to late frost, they are likely not to be exposed to damaging  
345 temperature (Fig. 4). Although climate models agree on the average trend, they are still unclear  
346 on the climate extreme events such as early and late frost events. Notably, the decennial  
347 damages (*i.e.* maximum damage occurring every ten years) may increase in North East and  
348 Massif Central area (Fig. S2). The relative balance between photo- and thermosensitivity is  
349 likely to be a critical trait explaining this trend. In the near future in these areas, minimum  
350 temperature are still likely to happen while dormancy induction and frost acclimation would be  
351 delayed by mean temperature increase.

352 Above the 14°C threshold, endodormancy induction and release would be more delayed than  
353 ecodormancy hastened, resulting in delayed budburst due to a lack of chilling, compared to the  
354 present situation. This situation would cover up to one quarter of France under RCP 8.5 scenario  
355 (Fig. 6). Although it would significantly reduce frost damages, even under false spring *scenarii*,  
356 lack of chilling would induce severe agronomic troubles such as erratic patterns of blooming,  
357 floribondity, and potential dischronism with anthesis. A similar pattern is also expected using  
358 fixed date (see Fig S3).

359 With respect to French nuts production, both IGP regions would face distinct threads. In the  
360 Périgord, chilling requirements are likely not to be met, and lower chilling varieties have to be  
361 selected, as the current ones do not exhibit variability for this trait (Charrier *et al.*, 2011). In  
362 Grenoble, earlier budburst dates are expected, leading to higher exposure to frost events, and

363 varieties with higher forcing requirements may help to stabilize the production (Charrier *et al.*,  
364 2018). However, both regions seem relatively safe with respect to frost damages.

## 365 **Conclusions and perspectives**

366 This study highlighted the relevance of dynamic dates for simulating annual phenological  
367 cycle and frost acclimation. The DORMPHOT model, integrating temperature and  
368 photoperiodic control of dormancy induction, is the most efficient for all studied processes. On  
369 one hand, higher decennial damages would be observed in the near future on *ca.* 15% of French  
370 territory because of late frost acclimation. On the other hand, the tipping point for phenological  
371 processes is likely to be reached during the XXI<sup>st</sup> century with chilling requirements that are  
372 likely not to be fulfilled. The correlation between MAT, phenological stages and frost damages  
373 is an important tool, to build relevant meta-models at the global scale.

374

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494

495 **Figure captions**

496 **Figure 1. A** Distribution of date at the onset of chilling accumulation  $T_0$  across France over the 1950-2005 period according to different  
497 computations:  $T_{\min}$  minimum temperature (lower than 15.28°C), DP DORMPHOT model from different sets of parameters (O: original,  
498 E early, L Late), LFT<sub>mod</sub> Leaf Fall model (thermal version modified), LFPT Leaf Fall model Photothermal version Original and modified.  
499 B, C and D  $T_0$  depending on mean annual temperature.

500 **Figure 2** MTB depending on Day after September 1<sup>st</sup> (A), DS according to DP<sub>ori</sub> (B), DS according to DP<sub>L</sub> (C).

501 **Figure 3. A-B.** Average dates of endodormancy release (A) and budburst (B) predicted across France under current climatic  
502 conditions. **C-D.** Average dates of endodormancy release (C) and budburst (D) depending on mean annual temperature (°C) across  
503 France.

504 **Figure 4. A-C.** Average frost damages predicted across France under current climatic conditions in autumn (A), winter (B) and  
505 spring (C). **D.** Average early frost damages depending on the average date of the first frost lower than 0°C. **E.** Average maximum  
506 frost damages depending on the average annual minimum temperature. **F.** Average late frost damages depending on the average  
507 date of the last frost lower than -4°C.

508 **Figure 5. A-C.** Average date of onset of dormancy (A), endodormancy release (B), budburst (C) over France depending on the  
509 mean annual temperature under current climate (gray), RCP 2.6 (2006-2051 cyan, 2051-2100 blue), RCP 4.5 (2006-2051 green,  
510 2051-2100 yellow), and RCP 8.5 *scenarii* (2006-2051 purple, 2051-2100 red). **D.** Average predicted autumn early frost damages  
511 depending on the date of first frost (<0°C) **E.** Average predicted maximum winter frost damages depending on the mean absolute  
512 minimum temperature **F.** Average predicted spring late frost damages depending on the date of last frost (<-4°C). Each dot  
513 represent the average of the considered period at 8 x 8km spatial resolution, black line represent the best non-linear regression.

514 **Figure 6.** Relative change in predicted average budburst date across France according to different climatic *scenarii* and time periods  
515 (earlier and later budburst dates than the mean are represented in blue and red, respectively).

516

517

518 **Table 1.** Site and dataset description

Location	Elevation (m asl.)	Latitude °	Longitude °	Mean annual temperature (°C)	Minimum temperature (°C)	Absolute minimum temperature (°C)	Number of freezing events	First Frost (Autumn) DOY	Last Frost (Spring) DOY	Number of observations (years and number of dates in brackets)					
										Endodormancy Release		Budburst		Frost Hardiness	
										Calibration	Validation	Calibration	Validation	Calibration	Validation
Balandran	69	43.758	4.516	16.90	12.00	-3.78	14.5	340	50	1	1	0	0	0	0
Chatte	304	45.143	5.282	13.62	8.15	-9.39	61.7	308	102	0	0	12	11	0	1 (6)
Creyse	115	44.887	1.597	14.65	8.52	-8.50	52.4	309	104	0	0	13	12	0	1 (8)
Crouël	340	45.779	3.142	13.25	9.26	-11.51	59.6	302	108	13	12	4	4	5 (49)	2 (21)
Orcival	1150	45.683	2.842	12.92	7.72	-12.13	97.4	291	126	1	1	1	0	0	0
Terrasson	90	45.136	1.300	14.61	8.96	-9.69	47.4	311	100	1	1	1	0	0	0
Theix	945	45.706	3.021	9.70	6.22	-15.11	100.3	282	129	1	1	1	0	1 (11)	1 (9)
Toulenne	22	44.557	-0.263	15.38	10.56	-6.09	25.9	325	74	1	0	9	9	0	0
Mas Bové	112	41.170	1.169	15.87	10.81	-4.05	14.9	343	47	0	0	0	0	0	1 (7)

519

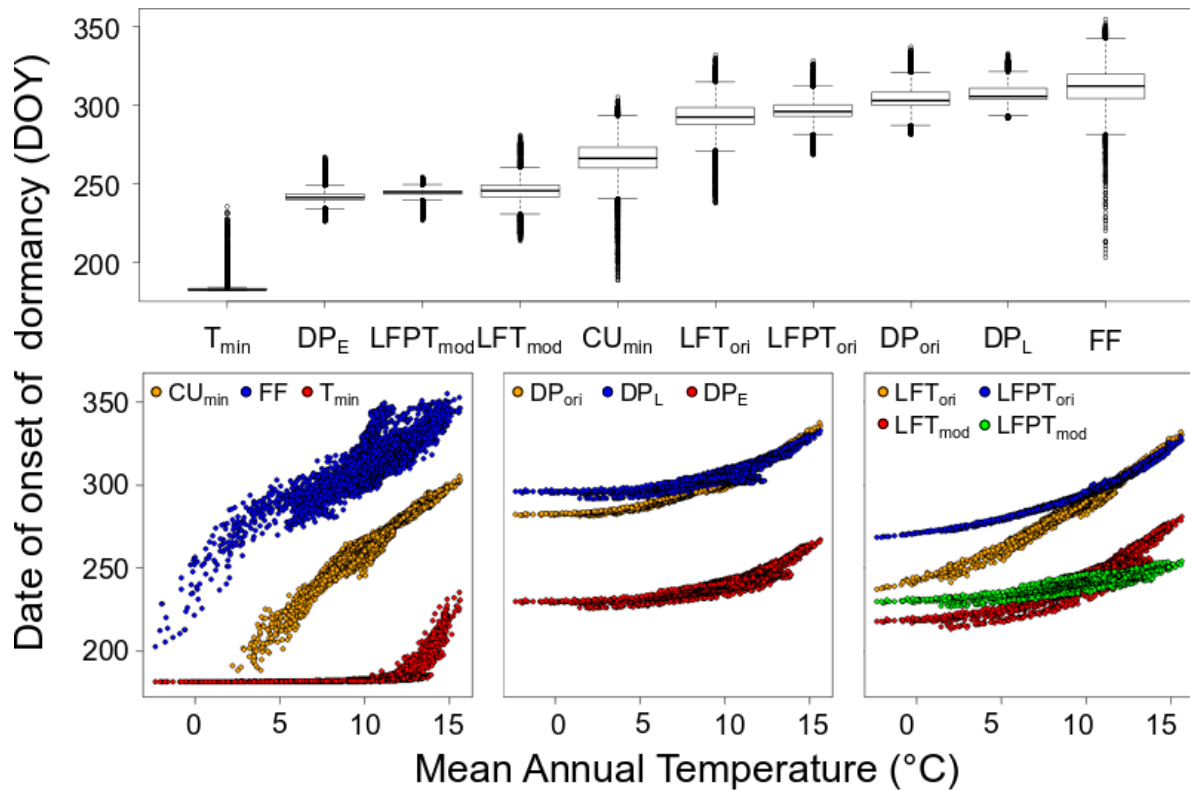
520



521 **Table 2.** Quality assessment of different models. RMSE(P) less than 15% higher than minimum RMSE or RMSEP are indicated in  
 522 bold.

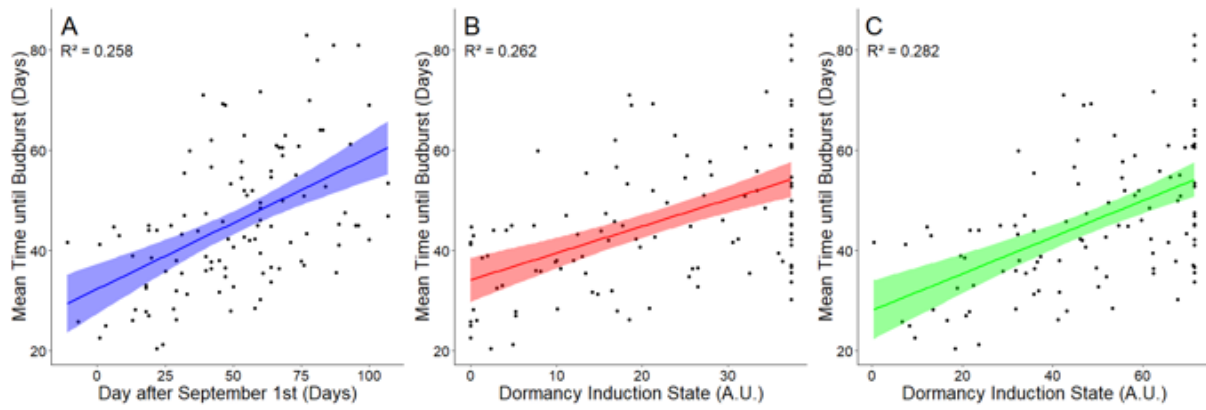
			Endodormancy	Budburst		Frost		PI	
			Release Date		Date		Hardiness		
Type	Function	D <sub>CA</sub>	RMSE	RMSEP	RMSE	RMSEP	RMSE	RMSEP	
			(days)	(days)	(days)	(days)	(°C)	(°C)	
Fixed		182 (Jul. 1 <sup>st</sup> )	<b>12.84</b>	11.84	8.58	8.08	<b>1.79</b>	3.52	7.31
		192 (Jul. 11 <sup>th</sup> )	<b>12.64</b>	11.48	8.44	<b>7.57</b>	<b>1.79</b>	3.39	7.10
		202 (Jul.21 <sup>st</sup> )	<b>12.41</b>	10.73	8.25	<b>7.28</b>	<b>1.80</b>	3.42	6.94
		213 (Aug. 1 <sup>st</sup> )	<b>12.33</b>	10.06	8.06	<b>7.14</b>	<b>1.79</b>	3.46	6.81
		223 (Aug. 11 <sup>th</sup> )	<b>12.65</b>	<b>9.36</b>	<b>7.78</b>	<b>6.89</b>	<b>1.78</b>	3.49	6.68
		233 (Aug. 21 <sup>st</sup> )	<b>12.68</b>	<b>8.71</b>	<b>7.61</b>	<b>6.85</b>	<b>1.78</b>	3.49	6.58
		244 (Sep. 1 <sup>st</sup> )	<b>12.87</b>	<b>8.75</b>	<b>7.39</b>	<b>7.03</b>	<b>1.79</b>	3.48	6.59
		254 (Sep. 11 <sup>th</sup> )	<b>13.19</b>	<b>8.49</b>	<b>7.26</b>	<b>6.88</b>	<b>1.77</b>	3.47	6.53
		264 (Sep. 21 <sup>st</sup> )	<b>13.70</b>	<b>8.80</b>	<b>7.15</b>	<b>7.24</b>	<b>1.74</b>	3.24	6.55
		274 (Oct. 1 <sup>st</sup> )	<b>13.80</b>	<b>8.47</b>	<b>7.25</b>	<b>7.38</b>	<b>1.73</b>	3.29	6.56
		284 (Oct. 11 <sup>th</sup> )	13.98	<b>8.29</b>	<b>7.10</b>	<b>6.93</b>	<b>1.77</b>	3.37	6.52
		294 (Oct. 21 <sup>st</sup> )	14.39	<b>8.47</b>	<b>7.25</b>	<b>7.15</b>	<b>1.84</b>	3.30	6.64
		305 (Nov. 1 <sup>st</sup> )	14.48	<b>9.22</b>	<b>7.45</b>	<b>7.47</b>	<b>1.84</b>	3.21	6.78
		315 (Nov. 11 <sup>th</sup> )	14.48	9.93	<b>7.52</b>	<b>7.56</b>	2.15	3.42	7.16
		325 (Nov. 21 <sup>st</sup> )	14.67	10.26	<b>7.46</b>	<b>7.43</b>	2.90	3.90	7.81
	335 (Dec. 1 <sup>st</sup> )	15.10	10.33	<b>7.58</b>	7.67	3.77	3.52	8.77	
Dynamic	Simple	FF	17.71	14.15	9.35	15.69	<b>1.90</b>	4.92	9.84
		T <sub>min</sub>	<b>12.88</b>	11.93	8.55	8.03	<b>1.79</b>	3.37	7.25
		T <sub>mean</sub>	<b>12.93</b>	11.59	8.70	8.47	<b>1.81</b>	3.38	7.31
		Photoperiod	<b>12.31</b>	10.24	<b>7.94</b>	<b>6.85</b>	<b>1.80</b>	3.46	6.78
	Complex	CU <sub>min</sub>	16.32	14.08	8.22	7.78	<b>1.78</b>	3.48	7.74
		LFT <sub>ori</sub>	<b>12.91</b>	10.37	<b>8.11</b>	<b>7.23</b>	<b>1.76</b>	3.22	6.81
		LFT <sub>mod</sub>	<b>12.57</b>	9.16	<b>8.11</b>	<b>7.23</b>	<b>1.80</b>	3.19	6.83
		LFPT <sub>ori</sub>	<b>13.34</b>	<b>8.67</b>	<b>7.42</b>	<b>6.72</b>	<b>1.83</b>	3.24	6.51
		LFPT <sub>mod</sub>	<b>12.66</b>	<b>8.81</b>	<b>7.43</b>	<b>6.89</b>	<b>1.78</b>	3.50	6.57
		DP <sub>ori</sub>	<b>13.01</b>	<b>8.81</b>	<b>7.47</b>	<b>6.61</b>	<b>1.76</b>	<b>2.87</b>	<b>6.31</b>
DP <sub>E</sub>		<b>12.05</b>	<b>8.64</b>	<b>7.73</b>	<b>7.24</b>	<b>1.80</b>	3.95	6.77	
DP <sub>L</sub>	<b>12.51</b>	<b>9.43</b>	<b>7.52</b>	<b>7.14</b>	<b>1.70</b>	<b>2.65</b>	<b>6.31</b>		

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**Figure 1. A** Distribution of date at the onset of chilling accumulation ( $D_{CA}$ ) across France over the 1950-2005 period according to different computations:  $T_{min}$  minimum temperature (lower than  $15.28^{\circ}C$ ),  $DP$  DORMPHOT model from different sets of parameters (O: original, E early, L Late),  $LFT_{mod}$  Leaf Fall model (thermal version modified),  $LFPT$  Leaf Fall model Photothermal version Original and modified. B, C and D  $T_0$  depending on mean annual temperature.

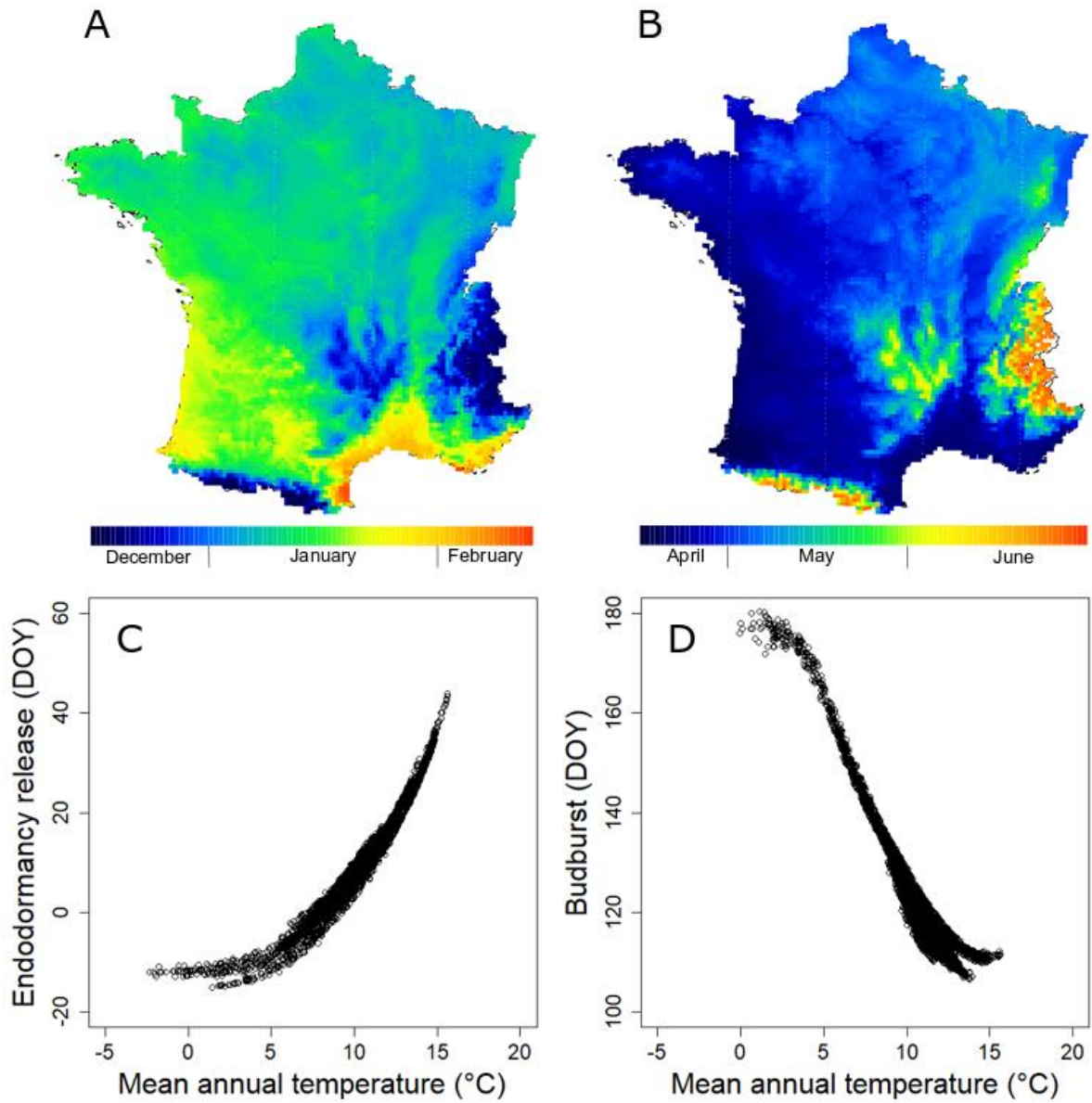


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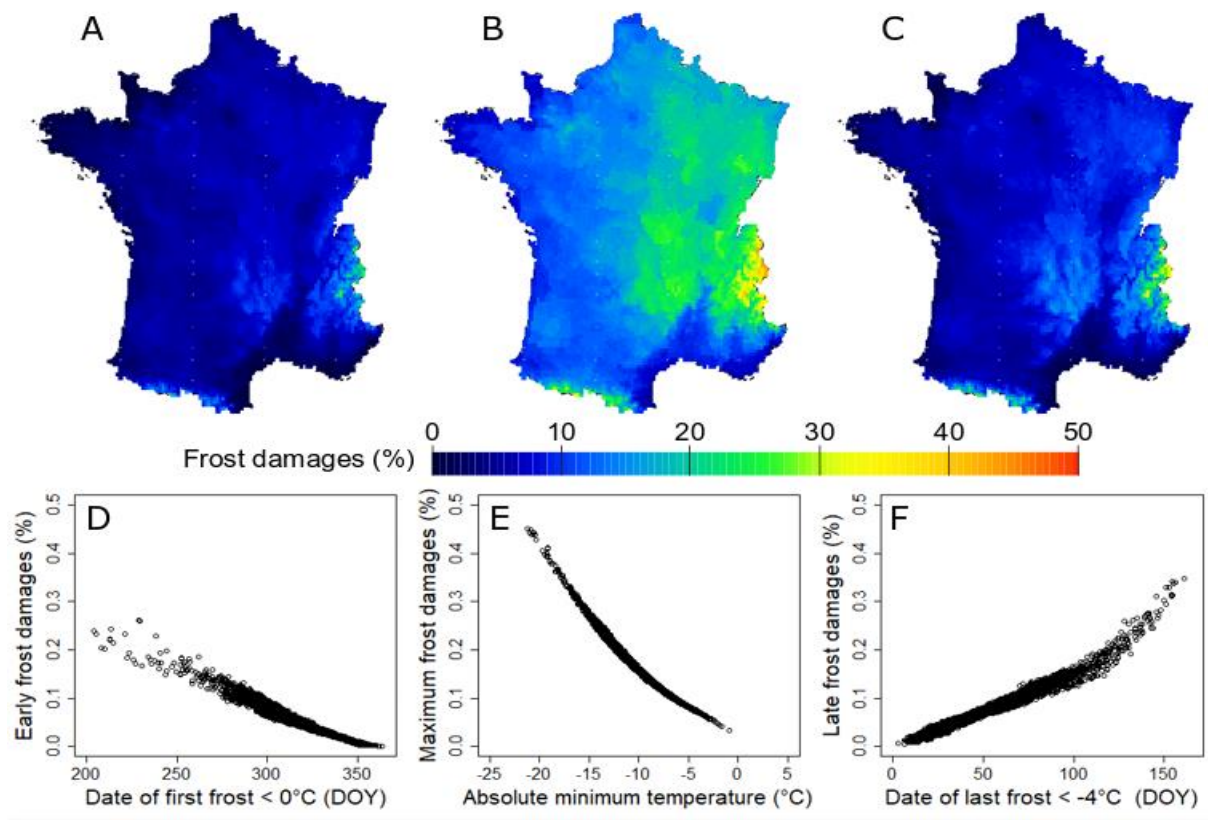
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**Figure 2.** Mean time until budburst in forcing test depending on Day after September 1<sup>st</sup> (A), DS according to  $DP_{ori}$  (B), DS according to  $DP_L$  (C).



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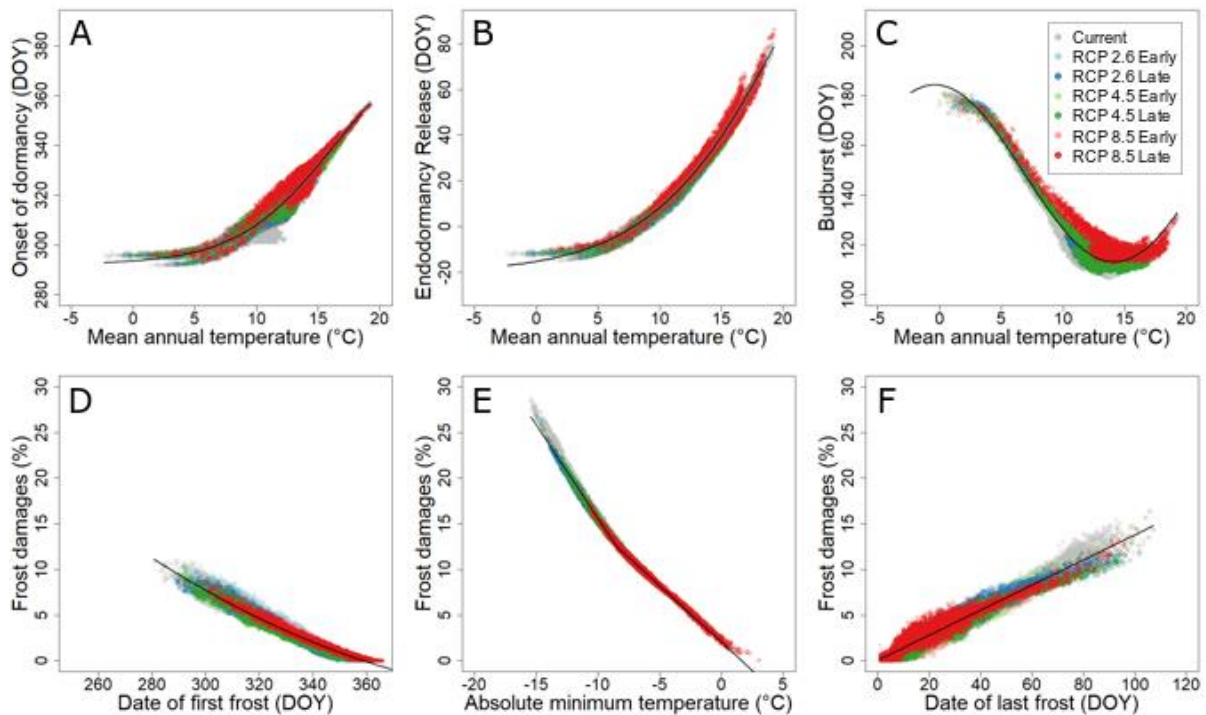
537 **Figure 3. A-B.** Average dates of endodormancy release (A) and budburst (B) predicted  
 538 across France under current climatic conditions. **C-D.** Average dates of endodormancy  
 539 release (C) and budburst (D) depending on mean annual temperature (°C) across  
 540 France.



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542 **Figure 4. A-C.** Average frost damages predicted across France under current climatic  
 543 conditions in autumn (A), winter (B) and spring (C). **D.** Average early frost damages  
 544 depending on the average date of the first frost lower than 0°C. **E.** Average maximum  
 545 frost damages depending on the average annual minimum temperature. **F.** Average  
 546 late frost damages depending on the average date of the last frost lower than -4°C.

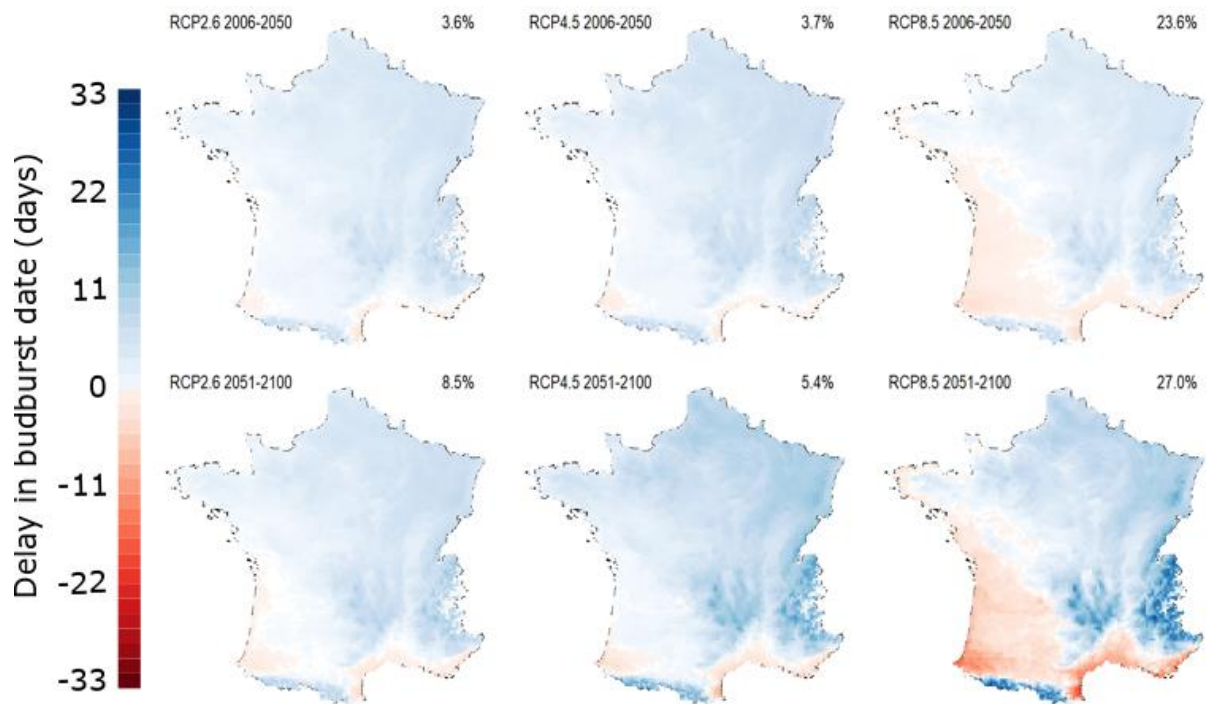
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549 **Figure 5. A-C.** Average date of onset of dormancy (A), endodormancy release (B),  
 550 budburst (C) over France depending on the mean annual temperature under current  
 551 climate (gray), RCP 2.6 (2006-2051 cyan, 2051-2100 blue), RCP 4.5 (2006-2051  
 552 green, 2051-2100 yellow), and RCP 8.5 *scenarii* (2006-2051 purple, 2051-2100 red).  
 553 **D.** Average predicted autumn early frost damages depending on the date of first frost  
 554 (<0°C) **E.** Average predicted maximum winter frost damages depending on the mean  
 555 absolute minimum temperature **F.** Average predicted spring late frost damages  
 556 depending on the date of last frost (<-4°C). Each dot represent the average of the  
 557 considered period at 8 x 8km spatial resolution, black line represent the best non-linear  
 558 regression.

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561 **Figure 6** Relative change in predicted average budburst date across France according  
 562 to different climatic *scenarii* and time periods. Earlier and later budburst dates than the  
 563 mean are represented in blue and red, respectively). The proportion of area showing  
 564 delayed budburst is indicated for each map.

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