Late autumn warming can both delay and advance spring budburst through contrasting effects on bud dormancy depth in Fagus sylvatica L.

Late autumn warming can both delay and advance spring budburst through contrasting effects on bud dormancy depth in *Fagus sylvatica* L.

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Running head: Impact of late fall warming on beech budburst

Abstract: The current state of knowledge on bud dormancy is limited. However, expanding such knowledge is crucial in order to properly model forest responses and feedback to future climate. Recent studies have shown that warming can decrease chilling accumulation and increase dormancy depth, thereby inducing delayed budburst in European beech (*Fagus sylvatica* L). Whether fall warming can advance spring phenology is unclear. To investigate the effect of warming on endodormancy of deciduous trees, we tested the impact of mild elevated temperature (+ 2.5-3.5 °C; temperature on average kept at 10 °C) in mid- and late autumn on bud dormancy depth and spring phenology of beech. We studied saplings by inducing periods of warming in greenhouses during two years. Even though warming reduced chilling in both years, we observed that the response of dormancy depth and spring budburst were year-specific. We found that warming during endodormancy peak could decrease bud dormancy depth and therefore advance spring budburst. This effect appears to be modulated by factors such as the date of senescence onset and forcing intensity during endodormancy. Results from this study suggest that not only chilling, but also forcing controls bud development during endodormancy, and that extra forcing in autumn can offset reduced chilling.

Keywords: Warming; Bud Dormancy; *Fagus sylvatica*; Chilling; Forcing; Endodormancy.

Abbreviations:

BB50	50% of open buds
BB90	90% of open buds
BB	Budburst
CCI	Chlorophyll Content Index
DOY	Day Of Year
BB01	First Bud open
GDD	Growing Degree Day

W	Warming temperature treatment
N	Normal ambient temperature treatment
Exp 1	Experiment 1, Year 2019-2020
Exp 2	Experiment 2, Year 2020-2021

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Introduction

Temperate forests represent 6% of the global land surface and contribute to 13% of the annual terrestrial carbon fixation (Pan et al., 2013; Saugier et al., 2001). Understanding the effect of climate change on temperate forest trees is therefore crucial in increasing our ability to project forest responses and feedbacks to the future climate.

Phenology is the study of recurring biological phenomena of living organisms on an annual basis (Dantec et al., 2014). Accordingly, it is a reliable indicator of interannual and interdecadal environmental changes such as climate change (Morin et al., 2009; Schwartz, 2003). For example, warming due to climate change has advanced the start of the growing season in many plant species (e.g. Menzel et al., 2006; Rötzer et al., 2004; Zohner and Renner, 2014). However, an earlier budburst (spring leaf-out) can also have a negative impact on the water cycle, as it induces earlier plant transpiration and soil moisture reduction, thereby increasing the probability of water deficiency (Lian et al., 2020).

Buds that produce the current year's leaves are made in the summer of the previous year. After completing growth, buds enter paradormancy in early autumn (Horvath et al., 2003). Subsequently, in late autumn, due to various environmental factors such as temperature and photoperiod, buds enter the endodormancy or "*winter dormancy*" stage (Singh et al., 2017). In order for endodormancy to end, a cold exposure known of as the "chilling requirement" is needed. In plants of the temperate zone, chilling occurs between -3.5 °C and 10 °C, but it seems to be most effective between 3.5 and 7.2 °C for various temperate tree species, including fruit trees (Čufar et al., 2012; Darbyshire et al., 2011; Sunley et al., 2006). Baumgarten et al. (2021) recently showed that temperatures from -2 to 10 °C are equally efficient for chilling beech. Moreover, some authors have suggested that the timing of senescence onset might also affect dormancy with a species-specific pattern (Fu et al., 2013; Marchand et al., 2020; Root et al., 2003). Early senescence, for instance, might allow earlier chilling accumulation and, indirectly, earlier endodormancy release in spruce and *Quercus robur L.* (pedunculate oak) (Dantec et al., 2014; Delpierre et al., 2017, 2016; Søgaard et al., 2008). Finally, in late winter, buds enter

the ecodormancy phase and start to accumulate heat (also called forcing), when temperature is above 5°C (Fu et al., 2013). Therefore, chilling corresponds to the cold exposure and forcing corresponds to heat exposure.

Dormancy depth is defined as the amount of heat needed for a tree under optimal growth conditions to release dormancy (Panchen et al., 2014; Vitasse et al., 2014). Dormancy depth is species dependent but, in general, increases progressively from fall (paradormancy) and achieves a peak between October and December (endodormancy) (Boyer and South, 1989; Calme et al., 1994; Malyshev, 2020). A high dormancy depth means that buds need more time (thus more heat accumulation) to burst (Dantec et al., 2014; Malyshev, 2020; Søgaard et al., 2009). Conversely, a low dormancy depth indicates that a tree is close to budburst (ecodormancy).

The chilling requirement generally describes cold exposure that is necessary for budburst of temperate forest trees (Arora et al., 2003; Calme et al., 1994; Harrington and Gould, 2015; Koo et al., 2014; Man et al., 2021, 2017). Lack of chilling during a warm winter delays budburst in many temperate trees. Interestingly, it has been shown that when the chilling requirement is not fulfilled it might be compensated by extra forcing accumulation (Campoy et al., 2019; Fu et al., 2013; Olsson et al., 2013; Olsson and Jönsson, 2014) that would allow the completion of bud development in the next spring. Forcing has typically been associated with ecodormancy. However, alternative assumptions have been proposed, for example that chilling and forcing accumulation are not separate, but play parallel roles in bud development, even during endodormancy (Chuine, 2000; Hänninen, 1990; Landsberg, 1974). In other words, chilling requirement and forcing requirement might work together to ensure that dormancy is broken timely in spring.

The impact of warming in late winter - early spring (ecodormancy) on budburst of temperate deciduous forest trees has been investigated extensively (Beil et al., 2021; Delpierre et al., 2017; Gordo and Sanz, 2005; Yang and Rudolf, 2010). Research has even been done on the effect of winter-spring warming on the budburst of the following year (Fu et al., 2012a; Liu et al., 2018; Malyshev, 2020; Root et al., 2003). Some experiments induced warming towards the end of

endodormancy in winter (e.g. December) (Dantec et al., 2014; Fu et al., 2012a, 2013; Heide, 2003) or in early autumn. For example, Malyshev (2020) showed that a warming of 10 days (+10 °C compared to ambient) in October increased dormancy depth in beech and birch, and delayed spring budburst in beech. Heide (2003) also showed that a warmer temperature in late summer - early autumn (August-October) of 10-20 °C increased the depth of dormancy and delayed budburst in birch and *Alnus glutinosa L. Gaertn* (alder). Beil et al. (2021) observed a delayed budburst for beech after a warming treatment of +2 °C in October. However, much less is known about the effect of warming during endodormancy only, i.e. mid-late autumn.

Using two years of experiments, we tested the impact of moderate (2.5 – 3.5 °C) autumnal warming on the dormancy depth and spring phenology of saplings of European beech. Our main hypothesis was that warming during endodormancy in mid- and late autumn, by decreasing the chilling accumulation, would delay the release of dormancy depth and induce a later budburst as observed in other warming experiments conducted in early autumn and with more intense warming. We studied key phenological and ecophysiological variables (e.g. onset of senescence, dormancy depth, timing of budburst) relevant before and after the temperature treatment (control and warming) during mid-late autumn. Additionally, we studied chilling and forcing accumulation before and during the warming treatment.

Materials and Methods

Study area and plant material

The study was conducted during 2 dormant seasons (2019-2020, experiment 1 (Exp1) and 2020-2021, experiment 2 (Exp2)) at an experimental site at the Drie Eiken Campus of the University of Antwerp, Belgium (51.161841N, 4.407150E). The location has a temperate climate, with maritime and subcontinental influences. In the last four decades, the mean annual precipitation was 840 mm (852 and 732 mm in 2019 and 2020, respectively) and the annual mean temperature was 11 °C (for both experimental years) (RMI 2019 ; RMI 2020; RMI 2021). Winters are cold but temperatures rarely drop below the freezing point and summers usually stay relatively cool. The coldest month is January (3 °C), whereas the warmest month is July (19 °C) (data from 1981-2020, RMI 2021).

According to the records from local meteorological stations, the mean temperature of November was 6.5 °C and 9.1 °C in 2019 and 2020, respectively, whereas the mean temperature of December was 5.8 °C in both years (Figure 1; Table S1). The temperature in the three weeks before the warming treatment was lower in 2019 than in 2020, with six and one nights with sub-zero temperatures, respectively. In addition, ambient temperature after temperature treatment was markedly different between the first and the second experiments. During the first year (2020), temperatures rarely dropped below 0 °C, only during four nights in January and two nights in February (with a minimum of -2 °C). During the second year (2021), subzero temperatures were measured on 8 nights in January and 9 nights in February (with a minimum of -8.8 °C). Moreover, February 2021 was on average 2.1 °C colder than February 2020 (Figure 1).

We bought beech saplings (80 cm to 1 m in height; 2 years old) from a local nursery. The official registration number of the provenance from the Institute for Nature and Forest Research (INBO) is 5WB0366 and the origin is Bois d'Hé / Coco. In February 2019 and 2020, the beech saplings were planted in 50 L pots with a soil composition of 10% peat and 90% sand (volume percentage). These pots were placed in climate controlled small greenhouses (*see below*). During the

growing season, all trees were watered three times a week. In both years, trees had an optimal amount of fertilizer, with a total of 70 g NPK (De Ceuster Meststoffen DCM Ecor NPK 8-5-6) and 3.6 g of micronutrients (DCM micro-mix) added per pot.

Senescence onset before manipulative treatment

The timing of leaf senescence onset was derived from weekly measurements of chlorophyll content decline (chlorophyll degradation) between late August and mid-November (Mariën et al., 2022, 2019). The chlorophyll content index (CCI) was measured using a chlorophyll content meter (CCM-200 plus; Opti-Sciences Inc., Hudson, NH, USA). We measured CCI on 9 randomly selected leaves, of which three where located at the top, three at the middle and three at the bottom part of each individual crown, on 8 trees and 38 trees in 2019 and 2020, respectively (Figure 1; Figure 2).

The senescence onset was derived from two parameters: (i) the 50% reduction of maximal CCI (50% CCI), and (ii) the breakpoint of the CCI decline series. The 50% CCI indicates the date (along the seasonal decline of CCI) when 50% of the maximal CCI value (measured at the start of the seasonal monitoring) is achieved. This determination is straightforward, but 50% CCI indicates an advanced stage of senescence rather than its onset (Mariën et al., 2019). Therefore, the time series of CCI data were also used to derive the date of senescence onset using a breakpoint analysis (Mariën et al., 2019). Before this analysis, extremely high (> 15 CCI units) and extremely low (<1 CCI units) data of CCI were considered as outliers and removed (0.70% of the complete data-set). The bulk of the CCI data were then analyzed separately per individual tree in each year with a piecewise regression model (R package '*segmented'*)(Muggeo, 2016). Following this procedure, we calculated two different linear models that fitted two different segments of the CCI pattern: one with a smaller slope, in absolute values, in late summer (slow degradation of chlorophyll before senescence) and one with a larger slope in early autumn (fast degradation of chlorophyll during senescence). The intersection of the two linear models (breakpoint) corresponded to the date on which there was a change in CCI trend, i.e. onset of leaf

senescence. However, of the total of the trees studied in both years (42), four had to be discarded from the final analyses because of anomalies in the CCI pattern or in the breakpoint identification procedure (e.g. no clear decline of CCI in autumn). In total, we were able to use 8 trees in 2019 and 34 trees in 2020. Analyses done with all trees (including extreme high and extremely low CCI values) are also reported (Table S2), but they had to be done on aggregated data (combination of all trees) and thus do not allow for standard statistical comparisons.

Climate-controlled greenhouses

We used 12 climate-controlled greenhouses, covering an area of ~1.5 m x 1.5 m, with the back of the structure 1.5 m high and the front 1.2 m high (Figure S1A). The roof was made of colorless polycarbonate (~4 mm thick plate). This type of material reduces the incoming light only by 20% and modifies the light spectrum only in the UV range (Kwon et al., 2017). The rear of the greenhouses could not be opened, whereas the three other lateral sides could be opened (before and after the experiment) or closed with transparent plastic foil (during the experiment). Each greenhouse was equipped with a sensor (QFA66, Siemens, Erlangen, Germany) to monitor the relative humidity (RH) and air temperature (T_a). In 2020, the height of the greenhouses was increased by 70 cm to better accommodate the trees, but the roof material (colorless polycarbonate) was retained (Figure S1B). A more detailed description of the setup of the greenhouses can be found in the literature (De Boeck et al., 2012; Mariën et al., 2021). None of these studies reported any effect of the greenhouse unit on the treatment.

Both temperature treatment experiments started approx. 1 month after the onset of senescence, when all trees had 100% fall/brown leaves, meaning that the senescence process had been completed at the start of the experiment (Dox et al., 2020; Mariën et al., 2019). However, as the end date for both experiments was set at 18 December, Exp1 was conducted for 28 days (20/11/2019-18/12/2019; 613 hours), while Exp2 was conducted for 38 days (10/11/2020-18/12/2020; 916 hours; complete senescence occurred earlier in 2020 than in 2019). We applied two different treatments: control or ambient

normal temperature (N) and warm temperature treatment (W). In N, the greenhouse temperature was set to automatically match the outside temperature, so as to have normal chilling and forcing. In W, we applied warming to reduce chilling.

The temperature treatments reported in the experimental design were repeated twice, in two separate experiments (Exp1: 2019; Exp2: 2020). In Exp1, temperatures were manually adjusted (3-7 times per day) to remain at 10 °C; in Exp2, this was automatized. For Exp1, on average, the warming applied was +3.6 °C, with a mean temperature for the W greenhouses of 10.4 °C (SE ± 0.06 °C) and a mean temperature for the N greenhouses of 6.8 °C (SE ± 0.06 °C) (Figure 1, Figure S2). In Exp2, we automatically maintained a constant temperature of 10 °C, to have more accurate constant temperature. On average in Exp2 the warming applied was +2.6 °C, with a mean temperature for the W greenhouses of 10.9 °C (SE ± 0.01 °C) and a mean temperature for the N greenhouses of 8.1 °C (SE ± 0.03 °C) (Figure 1, Figure S2). With this treatment, the chilling hours between – 3.5 and 7 °C were reduced by 88% and 83% in 2019 and 2020, respectively (Figure S3). Overall, for both experiments, the temperature during the majority of the hours (62% in 2019 and 78% in 2020) was > 10 °C, and thus not considered able to chill the buds (Baumgarten et al., 2021; Čufar et al., 2012; Sunley et al., 2006) (Figure S2, Figure S3).

In 2019, we had two greenhouses for N and two for W, with each greenhouse containing 8 trees. In 2020, we had six greenhouses for N and five for W (there were originally six W greenhouses, but one unfortunately failed), with each greenhouse hosting 16 trees. In addition to the experimental trees in the greenhouses, extra trees were kept under ambient conditions outside (about 70 in 2019-2020 and 190 in 2020-2021). These untreated trees were used to compare spring dynamics between the two years and check for the effect of the greenhouses on spring phenology dynamics.

Dormancy depth analysis

To study the effect of temperature on the phenology of plants, Growing Degree Days (GDD) is one of the most frequently "heat unit" used. The concept of heat units resulted from observations that plants do not grow below a threshold temperature (Esparza et al., 2007; Kesner and Anderson, 1986). Dormancy depth was measured as the accumulated GDD (*see below*) needed to induce budburst (dormancy release) when trees were placed in growth rooms at optimal growth conditions (16h of light (CDM-TP Elite MW; D-Papillon 315W, Light interaction Agro) from 6.00 till 22.00, approx. 22 °C day and night; 40-60% relative humidity) (Beil et al., 2021; Malyshev, 2020). Values of air temperature and humidity were logged in the chambers twice per hour. The accumulated GDD (*see below*) was recorded for the first bud to burst (BB01), when 50% of the buds had opened (BB50) and when 90% of the buds had opened (BB90). We used the bud developmental stages from Davi et al., (2011) (Figure S4). Dormancy depth was measured for trees in three conditions: (i) before temperature treatment, (ii) after temperature treatment and (iii) trees kept outside (no experimental trees) during the whole winter season.

After temperature treatment. Immediately after the temperature treatment (18 December), we placed experimental trees in the growth rooms to measure dormancy depth of the buds. In 2019, we analyzed 6 and 3 trees from N and W treatments, respectively. In 2020, 7 trees were used per treatment.

Before temperature treatment. Moreover, in order to verify the absence of significant greenhouses artifact effects, in 2020, dormancy depth was also measured (as described above) for W and N trees before the warming treatment had begun. These tests showed no relevant difference between greenhouses (see Figure S5).

Seasonal pattern. To determine the dormancy depth changes under ambient conditions of the study provenance during autumn-winter, we used potted trees kept outside (with the same fertilization level as the experimental trees). From December to March of 2019-2020 and from September to February of 2020-2021, every two or three weeks, three trees

were defoliated and put in the growth chambers at optimal growth conditions. Also for these trees, relative dormancy depth was estimated by the heat accumulated till BB01, measured as reported above.

Growing Degree Days

Dormancy depth was measured in Growing Degree Days (GDD, °C) required for a tree to open its buds under the optimal and standardized growing conditions of our growth chambers (Cannell and Smith, 1983; Halbritter et al., 2020; Heide, 1993; Murray et al., 1989). To determine GDD, we used the following formula:

$$GDD = \sum_{t0}^{BBdate} \begin{pmatrix} 0 & T_x \leq 5 \\ T_x - 5 & T_x > 5 \end{pmatrix} \qquad \text{Eq (1)}$$

Where *5°C* is the temperature threshold used in *Fagus sylvatica L.* phenological studies in temperate regions (Beil et al., 2021; Dantec et al., 2014; Fu et al., 2012a, 2013; Hänninen and Kramer, 2007; Murray et al., 1989); *BBdate* is the date of BB01, BB50 or BB90; and *Tx* is the daily mean temperature in the chamber and *t0* is the date when trees were placed in the growth chambers. The GDD accumulation occurred thus from t0 till BB01, BB50 and BB90. Using the same formula, GDD was also calculated for the W and N trees before (from senescence onset), during and after the temperate treatment till budburst to estimate the forcing requirement for spring budburst.

Spring budburst after manipulation

After the temperature treatment in 2019, the trees (n=7-8) of Exp1 that were not used for the dormancy depth study were put outside of the climate-controlled greenhouses and studied during the next spring to determine the timing of leaf out (also characterized by BB01, BB50 and BB90). On the other hand, in 2020, after the manipulation, the trees of Exp2 (n=16) not used for the dormancy depth analysis were kept till spring inside the greenhouses, automatically setting the temperature as the ambient temperature and exposing the trees only to LED lamps (Venntis Technologies, Total Grow Mezzo 85W, 47" Light Bar). The LED lights simulated the natural photoperiod regime, but their intensity and spectrum were different than that of the natural light. This setup was necessary in 2020 due to a parallel running experiment. The timing of budburst can thus not be compared between the two years. Nonetheless, as both N and W

treatments (in both years) were exposed to the exact same conditions (except temperature during November-December), the impact of the different warming treatments on spring budburst can be studied without bias.

Chilling

The chilling accumulation was calculated using three modelling approaches: the Sequential Model (SM), the Utah model (Utah) and the Unified Model (UM). As these models have different structure and parameterization, their comparison strengthens the estimated chilling patterns and trends.

(1) The Sequential Model (SM) derives from the Chilling Rate Model, developed by Sarvas (1974) and reformulated by Hänninen (1990) and Kramer (1994). The SM was found to be the most accurate model for predicting budburst dates of deciduous trees when chilling was considered (Fu et al., 2012b), even in experiments in which chilling and forcing were manipulated separately (Fu et al., 2012a). In this model, the chilling range is between -3.5 and 10.4 °C. We applied the SM parameterization used in previous studies for the same beech provenance used here following Fu et al. (2013):

$$Chilling\ (end\ date) = \sum_{t0}^{end\ date} \begin{pmatrix} 0 & T_x \leq -3.4 \\ 0 & T_x \geq 10.4 \\ 0.159 * T_x + 0.505 & -3.4 < T_x \leq 3.5 \\ -0.159 * T_x + 1.621 & 3.5 < T_x < 10.4 \end{pmatrix} \quad \text{Eq (2)}$$

Where Chilling (end date) represents the accumulated chilling over the analyzed period (in Chilling Units, CU) and T_x represents the average temperature per day.

(2) The Utah model (also known as Richardson model) is mostly used for observations in the field, for both crops and trees. The chilling range is between 1.4 and 12.4 °C. In contrast to the other two models, the Utah model reduces the chilling by high temperatures (>16 °C) and at an hourly, rather than daily, time intervals. The model equations are as follows with parameterization for peaches (*Prunus persica L.* Elberta and Redhaven (Richardson et al., 1974)):

$$Chilling\ (end\ date) = \sum_{t0}^{end\ date} \begin{cases} 0 & T_{xi} \leq 1.4 \\ 0.5 & 1.5 < T_{xi} < 2.4 \\ 1 & 2.5 < T_{xi} < 9.1 \\ 0.5 & 9.2 < T_{xi} < 12.4 \\ 0 & 12.5 < T_{xi} < 15.9 \\ -0.5 & 16 < T_{xi} < 17.9 \\ -1 & T_{xi} > 18 \end{cases} \quad \text{Eq (3)}$$

Note that for the Utah model, T_{xi} represents the hourly temperature in °C.

(3) The Unified Model was proposed by Chuine (2000) as an integration of the approaches used in other bud-burst models (Fu et al., 2012b). For the UM, we use the parameterization reported in Chuine et al. (2016). While it is not based on the studied species (beech) but on walnut (*Juglans regia* L.), this parameterization has the advantage of having been calibrated not only against bud-burst data (as the other models) but also against dormancy depth data (Table 1). The equation for the UM is as follows:

$$Chilling\ (end\ date) = \sum_{t0}^{end\ date} \left(\frac{1}{1+e^{a(Tx-c)^2+b(Tx-c)}}\right) \quad \text{Eq (4)}$$

Where *a*, *b* and *c* are species dependent constants.

For both the SM and the UM, different parameterizations were also tested (e.g. based on different species or, for UM, considering or not dormancy depth data in the model calibration). Whereas the absolute chilling unit values were different, these tests showed that the estimated chilling trends between W and N trees did not vary significantly when applying different parameterizations. Therefore, the results of these tests were only reported in Supplementary Data (Table S3) and not discussed further. Finally, note that in this study both the chilling scheme (see above in this paragraph) and the forcing scheme (see above in paragraph GDD) were used to provide simulations of chilling and forcing units for the whole dormant season, from senescence onset to budburst.

Statistical analysis

All statistical analyses were performed using the R software program environment (RStudio Inc, R version 4.2.0, GNU Affero General Public License v3). Packages *ChillR* (Luedeling, 2020) and *ChillModel* (Pertille et al., 2019) were used to

the model analysis based on Utah and UM model, respectively. We used one-way ANOVA (Exp1 and Exp2; factor: warming) to compare differences in dormancy depth (measured as GDD, in °C) and spring budburst (in DOY) following the warming treatments. Both analyses were repeated three times, considering as response variable BB01, BB50 and BB90. All analyses met the assumptions of normality (evaluated with the Shapiro test) and homoscedasticity (tested with Non-Constant Error Variance (*ncvTest*)) (Fox and Weisberg, 2019). We performed tests with mixed models (*nlme* package, (Pinheiro and Bates, 2000)) to analyze the effect of greenhouse as random factor on dormancy depth and spring budburst. As this effect was not significant, these results are presented only in Supplementary Data (Table S4). Moreover, we used a one-way ANOVA (factor: warming) to compare the number of hours with mean temperature between -3.5 and 3.5 °C, between 3.5 and 7 °C, between 7 and 10 °C, 10 and 12°C, and > 12 °C for the two warming treatments. Another one-way ANOVA with year as a factor was performed to compare 50% CCI and onset of senescence between 2019 and 2020. In all these cases, the normality and homoscedasticity requirements were met. Differences in budburst timing between N trees and potted trees kept outside were also determined for BB01 by means of a one-way ANOVA (Table S5).

Results

Analysis on untreated trees

Senescence dynamics. The progressive decline of the CCI of the outdoor plants over time and the onset of senescence, i.e. the point at which the degradation of chlorophyll started to accelerate, are shown in Figure 2. The senescence onset occurred significantly (ANOVA, $p=0.005$) earlier in 2019 (DOY 292, SE ±4) compared to 2020 (DOY 274 (±3)) (Figure 1, Figure 2). Also, the 50% CCI was significantly earlier (ANOVA, $p<0.001$) in 2020 compared to 2019 (DOY 306 and 299, respectively). For both years, the dates of senescence onset obtained with the single tree analysis were comparable to the dates of senescence onset determined on the aggregated data for all trees (Table S2).

Dormancy dynamics. Figure 3 shows the dormancy depth (in GDD, °C) of trees growing outside in ambient conditions. In 2020-2021, data were available for six months. Dormancy depth increased from the beginning of September until the end of October, when it stabilized till mid-December. Afterwards, the dormancy depth progressively decreased until the end of the analysis in mid-February. The data from the previous year 2019-2020 (available from December till March) confirmed the pattern of 2020-2021. Additionally, these data indicated that the temperature treatment occurred when trees were at their maximal dormancy depth (early November – mid-December), i.e. endodormancy.

Spring dynamics. By monitoring the untreated trees (always outside), we observed that BB01 occurred significantly later in 2021 (DOY 119 ± 0.4) compared to 2020 (DOY 112 ± 0.3) ($p<0.05$) (Table S5). The budburst of N trees was on DOY 113 ± 0.3 and DOY 123 ± 0.7 in spring 2020 (Exp1) and 2021 (Exp2), respectively (Table S5). These data indicates that, for each individual year, budburst in trees kept in controlled climate greenhouses was slightly, but significantly delayed compared to trees kept outside ($p<0.001$).

Temperature treatment

Chilling. During the temperature treatment, the W trees were subjected to less chilling. This was indicated consistently by all three chilling models used. However, the chilling dynamics were simulated differently across models. According to the SM, the reduction in chilling was smaller in the first than the second year (36% and 74%, respectively). On the other hand, N trees in 2019 received 1.5 time more chilling than N trees in 2020 (Table 1). Contrary to the SM, the Utah model simulated larger chilling reduction in the first than the second year (83% and 22%, respectively) but, like the SM, it also simulated larger chilling in 2019 than 2020 for the N trees (Table 1). The UM simulated smaller chilling reductions (approx. 15%) and smaller chilling in 2019 than 2020 for the N trees (Table 1). The models showed also different patterns of daily chilling accumulation during the warming period (Figure S6). The SM presented for W trees little chilling accumulation, and limited to few days, but increasing chilling for almost whole treatment period for N trees. On the other hand, the UM showed a very different pattern, with very constant chilling accumulation for the entire period for both W and N trees. The Utah model presented an intermediate behavior, with chilling simulations in 2019 similar to the SM and in 2020 more similar to the UM.

Dormancy depth. The depth of bud dormancy after the warming treatment is shown in Figure 4. In Exp1, the warming did not have any effect on the dormancy depth when this was assessed upon the first bud opening (BB01, $p=0.47$). However, the trees in the warming treatment required substantially more heat to fully open their crown, i.e. opening 50% or 90% of their buds ($p<0.01$). Thus, bud dormancy appeared to be delayed in W trees compared to N trees when it was assessed as BB50 and BB90. The direction of the warming effect in Exp2 was opposite than in Exp1, as in 2020-2021 trees subjected to W treatment needed less heat to release dormancy compared to trees in N treatment, thus with a smaller dormancy depth. This was valid when assessing bud dormancy depth with both BB01, BB50 and BB90 ($p<0.05$) (Figure 5, Table S4).

Spring phenology. Figure 5 reports on the spring phenology in the year following the autumnal temperature treatment. For Exp1, we observed that warming did not delay opening of the first bud, but it delayed budburst when 50% and 90% of the buds were considered (BB50, BB90; $p<0.05$). In fact, Exp1 showed that W treatment delayed BB50 by ~4 days and BB90% by ~6 days. For the Exp2, trees under W treatment had consistently an advanced spring phenology compared to N trees (BB01: $p < 0.001$; BB50: $p < 0.05$; BB90: $p < 0.05$). More precisely, Exp2 showed that the W treatment advanced the opening of the first bud by ~13 days, the opening of 50% of the buds by ~9 days and the opening of 90% of the buds by ~7 days.

Chilling and forcing from senescence onset till budburst

We investigated the effect of temperature treatment on W and N trees by analyzing forcing and chilling from the senescence onset until spring for both years using the SM model. To make the data interpretation easier, we present the chilling and forcing analysis in four phases: (1) from onset of senescence (breakpoint in CCI) till DOY 310 (early October to mid-November; period with low chilling); (2) from DOY 311 till DOY 325 (mid- to late November) when we can observe a progressive increment of the chilling accumulation, (3) from DOY 326 till DOY 353 (early to mid-December; period of warming experiment) (Figure 6) and (4) from DOY 353 till end of next May, after full completion of budburst (Figure S7).

Chilling. In the first phase, the buds did not accumulate a large amount of chilling in either year (Figure 4A) due to the outside temperature which was similar in both years and relatively warm (see October data in Table S1). In the second phase, a relatively large amount of chilling was accumulated in 2019 (approx. 15 chilling units, or CU), while in 2020 the chilling accumulation was much lower (approx. 3-4 CU). In fact, in the second phase the ambient temperature was colder in 2019 than in 2020 (a daily mean of 4.5 °C and 10.1 °C, respectively). In the third phase, the experimental warming was applied to impose a difference in CU between the temperature treatments. For both years, in fact, the N

trees obtained an higher amount of chilling than the W trees did (Table 1). In the last phase, chilling accumulation was higher in 2020 (57 CU in 2019 and 74 CU in 2020), as 2019 was warmer between mid-December and May (Table S6, Figure 4A, Figure S7 A and B).

Forcing. In the first phase, less forcing was accumulated in the first year than in the second year (110 °C vs. 250 °C). Also during the second phase, there was less forcing accumulation in the first (<10 °C) than the second year (~80 °C). In the third phase, in both years, the W trees accumulated a higher total amount of forcing (268 °C and 491 °C in 2019 and 2020, respectively), while the N trees accumulated, as expected, less forcing (182 °C and 394 °C in 2019 and 2020, respectively). Thus, in autumn 2020 the trees were subjected to less chilling (as shown previously) and more forcing (approx. 2 times more for both temperature treatments) (Figure 4B). In the last phase, as for the chilling, the forcing was rather gradual and similar between temperature treatments. During this period, the total forcing accumulation for W trees was 726 °C and 471 °C in the first and second year, respectively. These data match with the previous findings, as the period from December to May was warmer in 2019 than in 2020 (Table S6, Figure 4B, Figure S7 C and D).

Discussion

We applied here a warming treatment on *Fagus sylvatica* where temperature was kept on average at 10 °C during peak dormancy, the period during which warming effects on bud dormancy and phenology were unclear. Our experiments demonstrated that a relatively modest warming (+2.5 / +3.5 °C) in late autumn, during the dormancy peak, can significantly affect bud dormancy and spring phenology (budburst). In the first year the spring budburst was delayed and in the second year it was advanced by late autumn warming. Despite the relatively low number of replicates available (*see details below*), the results were consistent, showing e.g. a deeper dormancy depth associated with a later spring budburst and a lower dormancy associated with earlier spring budburst.

Based on previous research, it was expected that a warming treatment that reduced chilling in autumn would have increased bud dormancy and delayed budburst or alternatively have no effect (Caffarra and Donnelly, 2011; Campbell and Sugano, 1975; Fu et al., 2018; Malyshev, 2020; Root et al., 2003). In particular, Beil et al., (2021) showed that a warming during November and December had no effect on spring budburst in beech, pedunculate oak, birch and alder. While the general pattern described in the literature was observed during the first year of our study, in the second year we observed the opposite response, where warming reduced the dormancy depth and resulted in advanced budburst.

Two characteristics of the forcing conditions that occurred only in the second year might have induced the observed difference in impact of warming on endodormancy. First, because of the earlier senescence, forcing could have started earlier in 2020, allowing more forcing accumulation in early autumn. The connection between earlier senescence and early budburst has been recorded in previous studies (Delpierre et al., 2017; Marchand et al., 2020; Root et al., 2003). However, these authors postulated that earlier senescence would have allowed more chilling accumulation, while we show here that earlier senescence allows more forcing accumulation. It should be noted, however, that the relationship between the timing of senescence and peak dormancy is not clear. The second difference between both years was the

much greater forcing in mid- to late autumn in the second than in the first year, due to the warm conditions in November 2020. Thus, during endodormancy, more intense forcing might be needed to compensate for the lack of chilling in the same period. Moreover, we noticed that for the W trees of the second year, the amount of forcing accumulated from the senescence onset till the end of the warming treatment in mid-December was even larger than the amount of forcing accumulated between mid-December and May. Phytohormones can modulate dormancy and, in fact, applying exogenous phytohormones has an effect on dormancy release or entrance (e.g. Li et al., 2018; Molmann et al., 2005; Ophir et al., 2009; Rinne et al., 2011). For example, abscisic acid (ABA) maintains endodormancy whereas Gibberellins (GA) promote the dormancy release (e.g. Cooke et al., 2012; Molmann et al., 2005). Moreover, it has been shown that warming advances ecodormancy by reducing ABA concentration (Chmielewski and Götz, 2022; Larkindale et al., 2005). A similar mechanism might occur with warming during endodormancy. However, to clearly detect the mechanisms behind the advance of spring phenology following autumn warming and the exact role of phytohormones, molecular (e.g. transcriptomic) analyses should be performed. Note that the *Fagus sylvatica* genome was recently obtained and chromosomally annotated (Mishra et al., 2022, 2018) and a transcriptomic analysis of buds material from Exp1 and Exp2 is planned. Earlier phenology models assumed that the endodormancy of temperate deciduous trees is also sensitive to forcing accumulation (Hänninen, 1990; Kramer, 1994). For instance, the Parallel Model proposed by Landsberg (1974) assumes that forcing takes place even if the critical chilling accumulation value is not yet achieved. This model allows thus that chilling and forcing can increase together in time during endodormancy. More recent models, such as the UM, also consider concurrent chilling and forcing during endodormancy (Chuine, 2010; Chuine et al., 2016). Chilling and forcing are working simultaneously in buds, so temperatures can, in principle, both reduce and increase the dormancy depth (Malyshev, 2020, Harrington & Gould, 2015). However, to the best of our knowledge, there are no experimental reports on advancing of spring budburst as the result of autumn warming, thus of lower chilling and more forcing during

endodormancy. We already knew that more forcing can compensate for reduced chilling during ecodormancy in spring (Beil et al., 2021; Harrington et al., 2010; Malyshev, 2020; Pope et al., 2014). Here, we show that this compensation mechanism can also happen during endodormancy.

Another finding of the study is that the impact of a warming treatment on spring budburst (or on a variable measured through budburst dynamics, such as the dormancy depth) can be different when studied only on the opening of the first bud or when 50% of the buds are considered (Delpierre et al., 2017; Harrington and Gould, 2015; Malyshev et al., 2022). We additionally studied when trees had fully budburst (BB90) by calculating the exact percentage of bud bursting per trees. As spring phenology of the whole crown is more important than the spring phenology of a single bud, an important take-home message here is to also consider crown level measurements of spring leaf phenology as a response variable in manipulative experiments of leaf phenology dynamics, as shown by e.g. Campoy et al. (2019). The different bud dormancy dynamics triggered by autumn warming in the two years resulted also in a larger difference between BB50 and BB90 in the second year than the first year (see Figure 5). However, the possible reason for this difference remains unexplained.

We realize that our methodology had three drawbacks. (i) First, the design of the first year experiment was not ideal, with a minimal amount of replicates for some tests and without information on the seasonal variation of dormancy between September and November (a difference in the timing of peak dormancy in 2019 compared to 2020 cannot be ruled out). However, the results of the first year's experiment confirmed previous studies showing that autumn warming increases dormancy depth and delays bud burst in spring. Therefore, our overall conclusions are sound, as the unexpected and novel findings are from the second year's experiment, which was more complete and based on a larger amount of replicates. (ii) Second, the warming regime was slightly different between Exp1 and Exp2. In fact, in the second year's experiment, we introduced an automatic control of the temperature, with the result of having more stable

conditions (a constant temperature of 10 °C) than in the first year. Despite the fact that a constant autumn temperature (as in the warming treatment of 2020) does not occur in natural conditions, chilling typically varies between years, with years colder than others, with colder periods in different weeks of the winter or with years that feature more stable conditions than others. Nevertheless, chilling in years with very different temperature conditions can be compared by using the concept of chilling accumulation, considering different efficiency for chilling according to temperature and other modulators. Therefore, based on our current knowledge of these processes, the difference in warming treatment between years has been accounted for in the models used for the chilling calculation. The duration of the warming treatment was also different between years because we decided to use a phenological date (i.e. complete senescence, approx. 1 month after senescence onset) as a reference rather than a fixed date (e.g. 1/11). A fixed date would have made the experiments more comparable but it would have not taken into account the "real plant calendar". (iii) Third, caution should be taken when extrapolating our results to mature trees, as young trees have a lower chilling requirement and shallower dormancy than mature trees (see Fu et al., 2013 for data on beech). Measurements on both mature trees and young trees should be performed. Notwithstanding the methodological drawbacks indicated, the reliability of our results can be demonstrated by a detailed comparison with the literature. For example, the data of CCI and onset of leaf senescence for the experimental saplings in 2019 and 2020 are comparable with the same data recorded at our experimental platform in 2018 (Mariën et al., 2021) and for local stands of mature beech trees (Mariën et al., 2022). On the other hand, the observed seasonal dormancy pattern was very similar to the one recorded by Beil et al. (2021) on two-year-old European beech. Our values of peak dormancy depth were slightly larger than the ones reported by Beil et al. (2021), but of a comparable extent (approx. 900-1000 vs 750-800 GDD °C, respectively). Regarding budburst dates, estimates for the saplings kept outside (DOY 112 in 2020; for BB01) matched observations on trees from a local stand (DOY 111 in 2020; Dox et al. (2022)).

The chilling models applied in the study are widely used, but, due to their different structure, parameterization and chilling range, they provided different values of chilling rate and chilling accumulation over time and years. However, all models consistently indicated that warmed trees experienced lower chilling than the control trees for both years.

In conclusion, autumn warming can reduce dormancy depth and advance spring budburst. This phenomenon likely depends on the timing of autumn senescence, autumn temperature and potentially peak dormancy timing, all of which affect the forcing accumulation during autumn. The effect of these factors can, however, be subtle, as contrasting results have been found for different years. While more experiments involving multiple species and both young and mature trees (cutting) will be needed, our findings show previously unknown interactions between environmental conditions and tree seasonal dynamics and deepen our understanding of the functioning of temperate deciduous trees. Moreover, our results can serve as an important improvement to the budburst models used in, amongst others, the climate models. For instance, the use of dormancy depth data like those we presented should become a standard procedure in parameterizing bud burst schemes.

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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, 911–921. https://doi.org/10.21273/HORTSCI.38.5.911

Baumgarten, F., Zohner, C.M., Gessler, A., Vitasse, Y., 2021. Chilled to be forced: the best dose to wake up buds from winter dormancy. New Phytol. 230, 1366–1377. https://doi.org/10.1111/nph.17270

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. Glob. Change Biol. 27, 5806–5817. https://doi.org/10.1111/gcb.15858

Boyer, J.N., South, D.B., 1989. Seasonal changes in intensity of bud dormancy in loblolly pine seedlings. Tree Physiol. 5, 379–385. https://doi.org/10.1093/treephys/5.3.379

Caffarra, A., Donnelly, A., 2011. The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. Int. J. Biometeorol. 55, 711–721. https://doi.org/10.1007/s00484-010-0386-1

Calme, S., Bigras, F.J., Margolis, H.A., Hebert, C., 1994. Frost tolerance and bud dormancy of container-grown yellow birch, red oak and sugar maple seedlings. Tree Physiol. 14, 1313–1325. https://doi.org/10.1093/treephys/14.12.1313

Campbell, R.K., Sugano, A.I., 1975. Phenology of Bud Burst in Douglas-Fir Related to Provenance, Photoperiod, Chilling, and Flushing Temperature. Bot. Gaz. 136, 290–298. https://doi.org/10.1086/336817

Campoy, J.A., Darbyshire, R., Dirlewanger, E., Quero-García, J., Wenden, B., 2019. Yield potential definition of the chilling requirement reveals likely underestimation of the risk of climate change on winter chill accumulation. Int. J. Biometeorol. 63, 183–192. https://doi.org/10.1007/s00484-018-1649-5

Cannell, M.G.R., Smith, R.I., 1983. Thermal Time, Chill Days and Prediction of Budburst in Picea sitchensis. J. Appl. Ecol. 20, 951. https://doi.org/10.2307/2403139

Chmielewski, F.-M., Götz, K.-P., 2022. ABA and Not Chilling Reduces Heat Requirement to Force Cherry Blossom after Endodormancy Release. Plants 11, 2044. https://doi.org/10.3390/plants11152044

Chuine, I., 2010. Why does phenology drive species distribution? Philos. Trans. R. Soc. B Biol. Sci. 365, 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Chuine, I., 2000. A Unified Model for Budburst of Trees. J. Theor. Biol. 207, 337–347. https://doi.org/10.1006/jtbi.2000.2178

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. Glob. Change Biol. 22, 3444–3460. https://doi.org/10.1111/gcb.13383

Cooke, J.E.K., Eriksson, M.E., Junttila, O., 2012. The dynamic nature of bud dormancy in trees: environmental control and molecular mechanisms: Bud dormancy in trees. Plant Cell Environ. 35, 1707–1728. https://doi.org/10.1111/j.1365-3040.2012.02552.x

Čufar, K., De Luis, M., Saz, M.A., Črepinšek, Z., Kajfež-Bogataj, L., 2012. Temporal shifts in leaf phenology of beech (Fagus sylvatica) depend on elevation. Trees 26, 1091–1100. https://doi.org/10.1007/s00468-012-0686-7

Dantec, C.F., Vitasse, Y., Bonhomme, M., Louvet, J.-M., Kremer, A., Delzon, S., 2014. Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range. Int. J. Biometeorol. 58, 1853–1864. https://doi.org/10.1007/s00484-014-0787-7

Darbyshire, R., Webb, L., Goodwin, I., Barlow, S., 2011. Winter chilling trends for deciduous fruit trees in Australia. Agric. For. Meteorol. 151, 1074–1085. https://doi.org/10.1016/j.agrformet.2011.03.010

Davi, H., Gillmann, M., Ibanez, T., Cailleret, M., Bontemps, A., Fady, B., Lefèvre, F., 2011. Diversity of leaf unfolding dynamics among tree species: New insights from a study along an altitudinal gradient. Agric. For. Meteorol. 151, 1504–1513. https://doi.org/10.1016/j.agrformet.2011.06.008

De Boeck, H.J., De Groote, T., Nijs, I., 2012. Leaf temperatures in glasshouses and open-top chambers. New Phytol. 194, 1155–1164. https://doi.org/10.1111/j.1469-8137.2012.04117.x

Delpierre, N., Guillemot, J., Dufrêne, E., Cecchini, S., Nicolas, M., 2017. Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests. Agric. For. Meteorol. 234–235, 1–10. https://doi.org/10.1016/j.agrformet.2016.12.008

Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., Rathgeber, C.B.K., 2016. Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. Ann. For. Sci. 73, 5–25. https://doi.org/10.1007/s13595-015-0477-6

Dox, I., Gričar, J., Marchand, L.J., Leys, S., Zuccarini, P., Geron, C., Prislan, P., Mariën, B., Fonti, P., Lange, H., Peñuelas, J., Van den Bulcke, J., Campioli, M., 2020. Timeline of autumn phenology in temperate deciduous trees. Tree Physiol. 40, 1001–1013. https://doi.org/10.1093/treephys/tpaa058

Dox, I., Mariën, B., Zuccarini, P., Marchand, L.J., Prislan, P., Gričar, J., Flores, O., Gehrmann, F., Fonti, P., Lange, H., Peñuelas, J., Campioli, M., 2022. Wood growth phenology and its relationship with leaf phenology in deciduous forest trees of the temperate zone of Western Europe. Agric. For. Meteorol. 327, 109229. https://doi.org/10.1016/j.agrformet.2022.109229

Esparza, Gowda, Baumhardt, Marek, Howell, 2007. Heat Unit Availability for Cotton Production in the Ogallala Aquifer Region of the United States. J. Cotton Sci. 11, 110–117.

Fox, J., Weisberg, S., 2019. An R companion to applied regression, Third edition. ed. SAGE, Los Angeles.

Fu, Y.H., Campioli, M., Deckmyn, G., Janssens, I.A., 2013. Sensitivity of leaf unfolding to experimental warming in three temperate tree species. Agric. For. Meteorol. 181, 125–132. https://doi.org/10.1016/j.agrformet.2013.07.016

Fu, Y.H., Campioli, M., Deckmyn, G., Janssens, I.A., 2012a. The Impact of Winter and Spring Temperatures on Temperate Tree Budburst Dates: Results from an Experimental Climate Manipulation. PLoS ONE 7, e47324. https://doi.org/10.1371/journal.pone.0047324

Fu, Y.H., Campioli, M., Van Oijen, M., Deckmyn, G., Janssens, I.A., 2012b. Bayesian comparison of six different temperature-based budburst models for four temperate tree species. Ecol. Model. 230, 92–100. https://doi.org/10.1016/j.ecolmodel.2012.01.010

Fu, Y.H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Liu, Y., Sun, W., Janssens, I.A., Campioli, M., 2018. Larger temperature response of autumn leaf senescence than spring leaf-out phenology. Glob. Change Biol. 24, 2159–2168. https://doi.org/10.1111/gcb.14021

Gordo, O., Sanz, J.J., 2005. Phenology and climate change: a long-term study in a Mediterranean locality. Oecologia 146, 484–495. https://doi.org/10.1007/s00442-005-0240-z

Halbritter, A.H., De Boeck, H.J., Eycott, A.E., Reinsch, S., Robinson, D.A., Vicca, S., Berauer, B., Christiansen, C.T., Estiarte, M., Grünzweig, J.M., Gya, R., Hansen, K., Jentsch, A., Lee, H., Linder, S., Marshall, J., Peñuelas, J., Kappel Schmidt, I., Stuart-Haëntjens, E., Wilfahrt, P., the ClimMani Working Group, Vandvik, V., Abrantes, N., Almagro, M., Althuizen, I.H.J., Barrio, I.C., te Beest, M., Beier, C., Beil, I., Berry, Z.C., Birkemoe, T., Bjerke, J.W., Blonder, B., Blume-Werry, G., Bohrer, G., Campos, I., Cernusak, L.A., Chojnicki, B.H., Cosby, B.J., Dickman, L.T., Djukic, I., Filella, I., Fuchslueger, L., Gargallo-Garriga, A., Gillespie, M.A.K., Goldsmith, G.R., Gough, C., Halliday, F.W., Joar Hegland, S., Hoch, G., Holub, P., Jaroszynska, F., Johnson, D.M., Jones, S.B., Kardol, P., Keizer, J.J., Klem, K., Konestabo, H.S., Kreyling, J., Kröel-Dulay, G., Landhäusser, S.M., Larsen, K.S., Leblans,

N., Lebron, I., Lehmann, M.M., Lembrechts, J.J., Lenz, A., Linstädter, A., Llusià, J., Macias-Fauria, M., Malyshev, A.V., Mänd, P., Marshall, M., Matheny, A.M., McDowell, N., Meier, I.C., Meinzer, F.C., Michaletz, S.T., Miller, M.L., Muffler, L., Oravec, M., Ostonen, I., Porcar-Castell, A., Preece, C., Prentice, I.C., Radujković, D., Ravolainen, V., Ribbons, R., Ruppert, J.C., Sack, L., Sardans, J., Schindlbacher, A., Scoffoni, C., Sigurdsson, B.D., Smart, S., Smith, S.W., Soper, F., Speed, J.D.M., Sverdrup-Thygeson, A., Sydenham, M.A.K., Taghizadeh-Toosi, A., Telford, R.J., Tielbörger, K., Töpper, J.P., Urban, O., Ploeg, M., Van Langenhove, L., Večeřová, K., Ven, A., Verbruggen, E., Vik, U., Weigel, R., Wohlgemuth, T., Wood, L.K., Zinnert, J., Zurba, K., 2020. The handbook for standardized field and laboratory measurements in terrestrial climate change experiments and observational studies (ClimEx). Methods Ecol. Evol. 11, 22–37. https://doi.org/10.1111/2041-210X.13331

Hänninen, H., 1990. Modelling bud dormancy release in trees from cool and temperate regions. Acta For. Fenn. 0. https://doi.org/10.14214/aff.7660

Hänninen, H., Kramer, K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. Silva Fenn. 41. https://doi.org/10.14214/sf.313

Harrington, C.A., Gould, P.J., 2015. Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. Front. Plant Sci. 6. https://doi.org/10.3389/fpls.2015.00120

Harrington, C.A., Gould, P.J., St.Clair, J.B., 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. For. Ecol. Manag. 259, 798–808. https://doi.org/10.1016/j.foreco.2009.06.018

Heide, O.M., 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. Tree Physiol. 23, 931–936. https://doi.org/10.1093/treephys/23.13.931

Heide, O.M., 1993. Dormancy release in beech buds (Fagus sylvatica) requires both chilling and long days. Physiol. Plant. 89, 187–191. https://doi.org/10.1111/j.1399-3054.1993.tb01804.x

Horvath, D.P., Anderson, J.V., Chao, W.S., Foley, M.E., 2003. Knowing when to grow: signals regulating bud dormancy. Trends Plant Sci. 8, 534–540. https://doi.org/10.1016/j.tplants.2003.09.013

Kesner, R., Anderson, J.L., 1986. Validation of chill unit and flower bud phenology models for “Montmorency” sour Cherry. Acta Hortic 184 71-78. https://doi.org/10.17660/ActaHortic.1986.184.7

Koo, K.A., Patten, B.C., Teskey, R.O., Creed, I.F., 2014. Climate change effects on red spruce decline mitigated by reduction in air pollution within its shrinking habitat range. Ecol. Model. 293, 81–90. https://doi.org/10.1016/j.ecolmodel.2014.07.017

Kramer, K., 1994. Selecting a Model to Predict the Onset of Growth of Fagus sylvatica. J. Appl. Ecol. 31, 172. https://doi.org/10.2307/2404609

Kwon, Khoshimkhujaev, Lee, Yu, Park, Choi, 2017. Growth and Yield of Tomato and Cucumber Plants in Polycarbonate or Glass Greenhouses. Korean J. Hortic. Sci. 35. https://doi.org/10.12972/kjhst.20170009

Landsberg, J.J., 1974. Apple Fruit Bud Development and Growth; Analysis and an Empirical Model. Ann. Bot. 38, 1013–1023. https://doi.org/10.1093/oxfordjournals.aob.a084891

Larkindale, J., Hall, J.D., Knight, M.R., Vierling, E., 2005. Heat Stress Phenotypes of Arabidopsis Mutants Implicate Multiple Signaling Pathways in the Acquisition of Thermotolerance. Plant Physiol. 138, 882–897. https://doi.org/10.1104/pp.105.062257

Li, J., Xu, Y., Niu, Q., He, L., Teng, Y., Bai, S., 2018. Abscisic Acid (ABA) Promotes the Induction and Maintenance of Pear (Pyrus pyrifolia White Pear Group) Flower Bud Endodormancy. Int. J. Mol. Sci. 19, 310. https://doi.org/10.3390/ijms19010310

Lian, X., Piao, S., Li, L.Z.X., Li, Y., Huntingford, C., Ciais, P., Cescatti, A., Janssens, I.A., Peñuelas, J., Buermann, W., Chen, A., Li, X., Myneni, R.B., Wang, X., Wang, Y., Yang, Y., Zeng, Z., Zhang, Y., McVicar, T.R., 2020. Summer

soil drying exacerbated by earlier spring greening of northern vegetation. Sci. Adv. 6, eaax0255. https://doi.org/10.1126/sciadv.aax0255

Liu, Q., Piao, S., Janssens, I.A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R.B., Peñuelas, J., Wang, T., 2018. Extension of the growing season increases vegetation exposure to frost. Nat. Commun. 9, 426. https://doi.org/10.1038/s41467-017-02690-y

Luedeling, E., 2020. Future chill risk assessment using chillR. Acta Hortic. 225–232. https://doi.org/10.17660/ActaHortic.2020.1280.31

Malyshev, A.V., 2020. Warming Events Advance or Delay Spring Phenology by Affecting Bud Dormancy Depth in Trees. Front. Plant Sci. 11, 856. https://doi.org/10.3389/fpls.2020.00856

Malyshev, A.V., van der Maaten, E., Garthen, A., Maß, D., Schwabe, M., Kreyling, J., 2022. Inter-Individual Budburst Variation in Fagus sylvatica Is Driven by Warming Rate. Front. Plant Sci. 13, 853521. https://doi.org/10.3389/fpls.2022.853521

Man, R., Lu, P., Dang, Q.-L., 2021. Effects of insufficient chilling on budburst and growth of six temperate forest tree species in Ontario. New For. 52, 303–315. https://doi.org/10.1007/s11056-020-09795-1

Man, R., Lu, P., Dang, Q.-L., 2017. Insufficient Chilling Effects Vary among Boreal Tree Species and Chilling Duration. Front. Plant Sci. 8, 1354. https://doi.org/10.3389/fpls.2017.01354

Marchand, L.J., Dox, I., Gričar, J., Prislan, P., Leys, S., Van den Bulcke, J., Fonti, P., Lange, H., Matthysen, E., Peñuelas, J., Zuccarini, P., Campioli, M., 2020. Inter-individual variability in spring phenology of temperate deciduous trees depends on species, tree size and previous year autumn phenology. Agric. For. Meteorol. 290, 108031. https://doi.org/10.1016/j.agrformet.2020.108031

Mariën, B., Balzarolo, M., Dox, I., Leys, S., Lorène, M.J., Geron, C., Portillo-Estrada, M., AbdElgawad, H., Asard, H., Campioli, M., 2019. Detecting the onset of autumn leaf senescence in deciduous forest trees of the temperate zone. New Phytol. 224, 166–176. https://doi.org/10.1111/nph.15991

Mariën, B., Dox, I., De Boeck, H.J., Willems, P., Leys, S., Papadimitriou, D., Campioli, M., 2021. Does drought advance the onset of autumn leaf senescence in temperate deciduous forest trees? Biogeosciences 18, 3309–3330. https://doi.org/10.5194/bg-18-3309-2021

Mariën, B., Papadimitriou, D., Kotilainen, T., Zuccarini, P., Dox, I., Verlinden, M., Heinecke, T., Mariën, J., Willems, P., Decoster, M., Gascó, A., Lange, H., Peñuelas, J., Campioli, M., 2022. Timing leaf senescence: A generalized additive models for location, scale and shape approach. Agric. For. Meteorol. 315, 108823. https://doi.org/10.1016/j.agrformet.2022.108823

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern: European Phenological respinse to climate change. Glob. Change Biol. 12, 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Mishra, B., Gupta, D.K., Pfenninger, M., Hickler, T., Langer, E., Nam, B., Paule, J., Sharma, R., Ulaszewski, B., Warmbier, J., Burczyk, J., Thines, M., 2018. A reference genome of the European beech (Fagus sylvatica L.). GigaScience 7. https://doi.org/10.1093/gigascience/giy063

Mishra, B., Ulaszewski, B., Meger, J., Aury, J.-M., Bodénès, C., Lesur-Kupin, I., Pfenninger, M., Da Silva, C., Gupta, D.K., Guichoux, E., Heer, K., Lalanne, C., Labadie, K., Opgenoorth, L., Ploch, S., Le Provost, G., Salse, J., Scotti, I., Wötzel, S., Plomion, C., Burczyk, J., Thines, M., 2022. A Chromosome-Level Genome Assembly of the European

Beech (Fagus sylvatica) Reveals Anomalies for Organelle DNA Integration, Repeat Content and Distribution of SNPs. Front. Genet. 12, 691058. https://doi.org/10.3389/fgene.2021.691058

Molmann, J.A., Asante, D.K.A., 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 Environ. 28, 1579–1588. https://doi.org/10.1111/j.1365-3040.2005.01395.x

Morin, X., Lechowicz, M.J., Augspurger, C., O'Keefe, J., Viner, D., Chuine, I., 2009. Leaf phenology in 22 North American tree species during the 21st century. Glob. Change Biol. 15, 961–975. https://doi.org/10.1111/j.1365-2486.2008.01735.x

Muggeo, V.M.R., 2016. Testing with a nuisance parameter present only under the alternative: a score-based approach with application to segmented modelling. J. Stat. Comput. Simul. 86, 3059–3067. https://doi.org/10.1080/00949655.2016.1149855

Murray, M.B., Cannell, M.G.R., Smith, R.I., 1989. Date of Budburst of Fifteen Tree Species in Britain Following Climatic Warming. J. Appl. Ecol. 26, 693. https://doi.org/10.2307/2404093

Olsson, C., Bolmgren, K., Lindström, J., Jönsson, A.M., 2013. Performance of tree phenology models along a bioclimatic gradient in Sweden. Ecol. Model. 266, 103–117. https://doi.org/10.1016/j.ecolmodel.2013.06.026

Olsson, C., Jönsson, A.M., 2014. Process-based models not always better than empirical models for simulating budburst of Norway spruce and birch in Europe. Glob. Change Biol. 20, 3492–3507. https://doi.org/10.1111/gcb.12593

Ophir, R., Pang, X., Halaly, T., Venkateswari, J., Lavee, S., Galbraith, D., Or, E., 2009. Gene-expression profiling of grape bud response to two alternative dormancy-release stimuli expose possible links between impaired mitochondrial activity, hypoxia, ethylene-ABA interplay and cell enlargement. Plant Mol. Biol. 71, 403. https://doi.org/10.1007/s11103-009-9531-9

Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The Structure, Distribution, and Biomass of the World's Forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

Panchen, Z.A., Primack, R.B., Nordt, B., Ellwood, E.R., Stevens, A., Renner, S.S., Willis, C.G., Fahey, R., Whittemore, A., Du, Y., Davis, C.C., 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. New Phytol. 203, 1208–1219. https://doi.org/10.1111/nph.12892

Pertille, R.H., Sachet, M.R., Guerrezi, M.T., Citadin, I., 2019. An R package to quantify different chilling and heat models for temperate fruit trees. Comput. Electron. Agric. 167, 105067. https://doi.org/10.1016/j.compag.2019.105067

Pinheiro, Bates, 2000. Mixed-Effects Models in S and S-PLUS, Statistics and Computing. Springer-Verlag, New York. https://doi.org/10.1007/b98882

Pope, K.S., Da Silva, D., Brown, P.H., DeJong, T.M., 2014. A biologically based approach to modeling spring phenology in temperate deciduous trees. Agric. For. Meteorol. 198–199, 15–23. https://doi.org/10.1016/j.agrformet.2014.07.009

Richardson, E., Seeley, S.D., Walker, D.R., 1974. A Model for Estimating the Completion of Rest for 'Redhaven' and 'Elberta' Peach Trees1. HortScience 9, 331–332. https://doi.org/10.21273/HORTSCI.9.4.331

Rinne, P.L.H., Welling, A., Vahala, J., Ripel, L., Ruonala, R., Kangasjärvi, J., van der Schoot, C., 2011. Chilling of Dormant Buds Hyperinduces FLOWERING LOCUS T and Recruits GA-Inducible 1,3-β-Glucanases to Reopen Signal Conduits and Release Dormancy in Populus. Plant Cell 23, 130–146. https://doi.org/10.1105/tpc.110.081307

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60. https://doi.org/10.1038/nature01333

Rötzer, T., Grote, R., Pretzsch, H., 2004. The timing of bud burst and its effect on tree growth. Int. J. Biometeorol. 48, 109–118. https://doi.org/10.1007/s00484-003-0191-1

Sarvas, R., 1974. Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. Metsantutkimuslaitoksen Julk. 84, 101–101.

Saugier, B., Roy, J., Mooney, H.A., 2001. Estimations of Global Terrestrial Productivity, in: Terrestrial Global Productivity. Elsevier, pp. 543–557. https://doi.org/10.1016/B978-012505290-0/50024-7

Schwartz, M.D., 2003. Phenology: an integrative environmental science, Tasks for vegetation science. Kluwer academic publ, Dordrecht Boston London.

Singh, R.K., Svystun, T., AlDahmash, B., Jönsson, A.M., Bhalerao, R.P., 2017. Photoperiod- and temperature-mediated control of phenology in trees – a molecular perspective. New Phytol. 213, 511–524. https://doi.org/10.1111/nph.14346

Søgaard, G., Granhus, A., Johnsen, Ø., 2009. Effect of frost nights and day and night temperature during dormancy induction on frost hardiness, tolerance to cold storage and bud burst in seedlings of Norway spruce. Trees 23, 1295–1307. https://doi.org/10.1007/s00468-009-0371-7

Søgaard, G., Johnsen, Ø., Nilsen, J., Junttila, O., 2008. Climatic control of bud burst in young seedlings of nine provenances of Norway spruce. Tree Physiol. 28, 311–320. https://doi.org/10.1093/treephys/28.2.311

Sunley, R.J., Atkinson, C.J., Jones, H.G., 2006. Chill unit models and recent changes in the occurrence of Winter chill and Spring frost in the United Kingdom. J. Hortic. Sci. Biotechnol. 81, 949–958. https://doi.org/10.1080/14620316.2006.11512181

Vitasse, Y., Lenz, A., KÃ¶rner, C., 2014. The interaction between freezing tolerance and phenology in temperate deciduous trees. Front. Plant Sci. 5. https://doi.org/10.3389/fpls.2014.00541

Yang, L.H., Rudolf, V.H.W., 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecol. Lett. 13, 1–10. https://doi.org/10.1111/j.1461-0248.2009.01402.x

Zohner, C.M., Renner, S.S., 2014. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecol. Lett. 17, 1016–1025. https://doi.org/10.1111/ele.12308

Figures and tables:

Table 1 : Modeling of chilling units. Chilling units calculated with different models during the experimental period. W: warming treatment and N: normal temperature treatment.

Model	Key reference model	Parameterization dataset	Time step	Chilling units 2019		Chilling units 2020	
				N	W	N	W
SM	Sarvas (1974), Hänninen (1990) Kramer (1994)	Budburst of beech (same provenance as in this study) (Fu et al., 2013)	daily	28.2	18.0	18.1	4.7
Utah	Richardson et al. (1974)	Budburst of peach (Richardson et al., 1974)	hourly	6465	1076	2334	1817
UM	Chuine (2000; Chuine et al. (2016)	Budburst and dormancy depth of walnut (Chuine et al.,2016)	daily	21.2	17.6	25.9	22.7

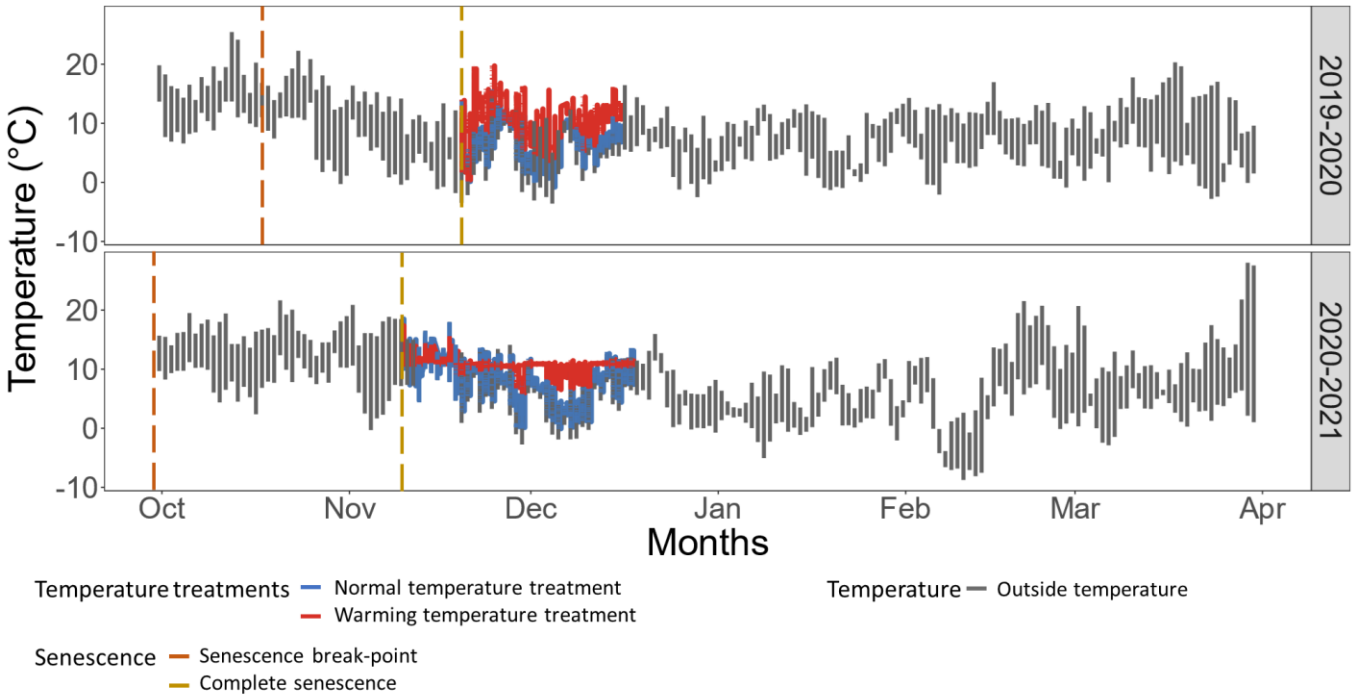

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Figure 1: Average, minimum and maximum daily temperature in 2019– 2020 and 2020-2021 during October – March for outside and experimental conditions. Daily temperature, outside, with bars indicating the minimum and maximum temperature daily recorded between October and March of 2019-2020 and 2020-2021 (grey). Blue line (N, normal temperature treatment) and red line (W, warming temperature treatment) indicate the temperature inside the climate controlled greenhouses for 28 days (20/11/2019-18/12/2019) in 2019 (Exp1) and for 38 days (10/11/2020-18/12/2020) in 2020 (Exp2). The orange vertical dashed line represents the senescence break point (or senescence onset), while the dark yellow vertical dashed line represents the complete senescence and start of the temperature treatment.

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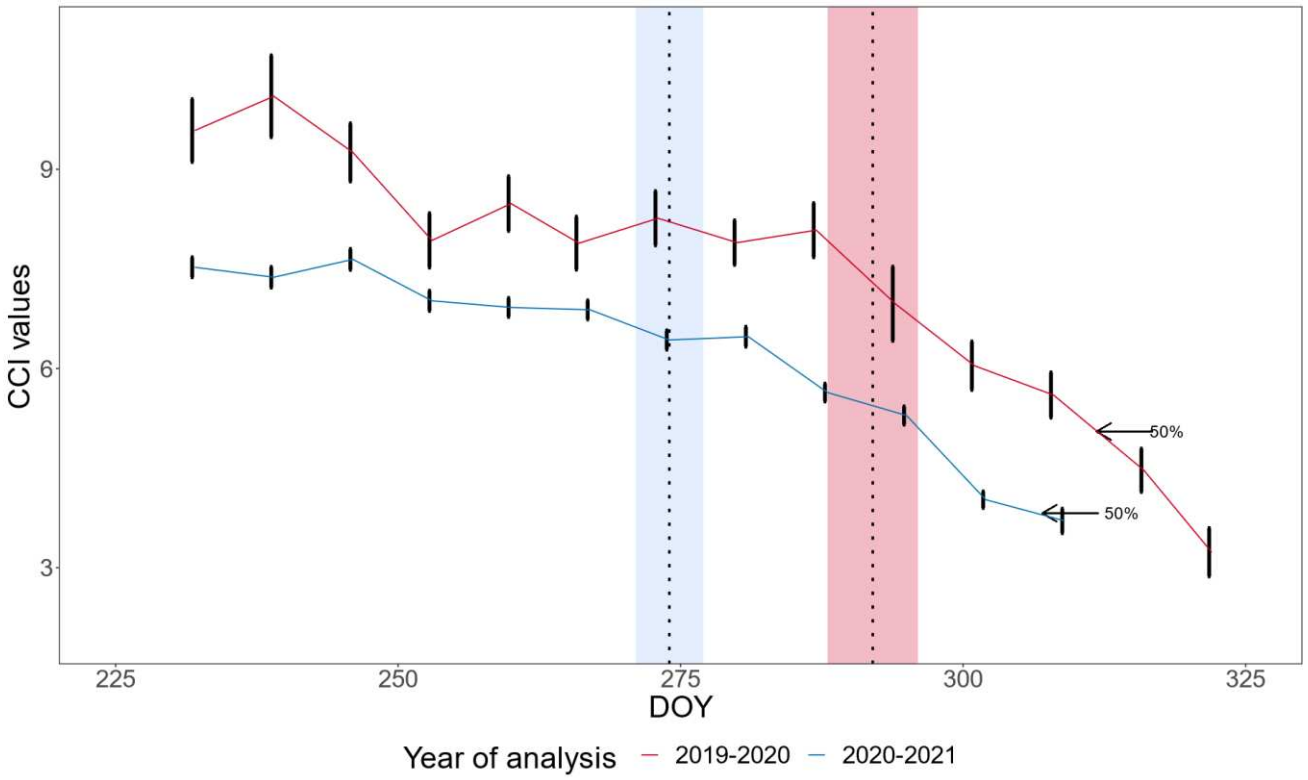

Figure 2: Senescence dynamics and senescence onset before temperature treatment based on the chlorophyll content index (CCI) seasonal decline and breakpoint analysis. The lines (red for Exp1 and blue for Exp2) connect mean values of CCI (± SE) across trees (in 2019 n=8, in 2020 n=38). The vertical dotted lines represent the dates of 'onset of senescence' (breakpoint), while the shaded areas indicate their uncertainty (± SE). Arrows: date of 50% of CCI decline.

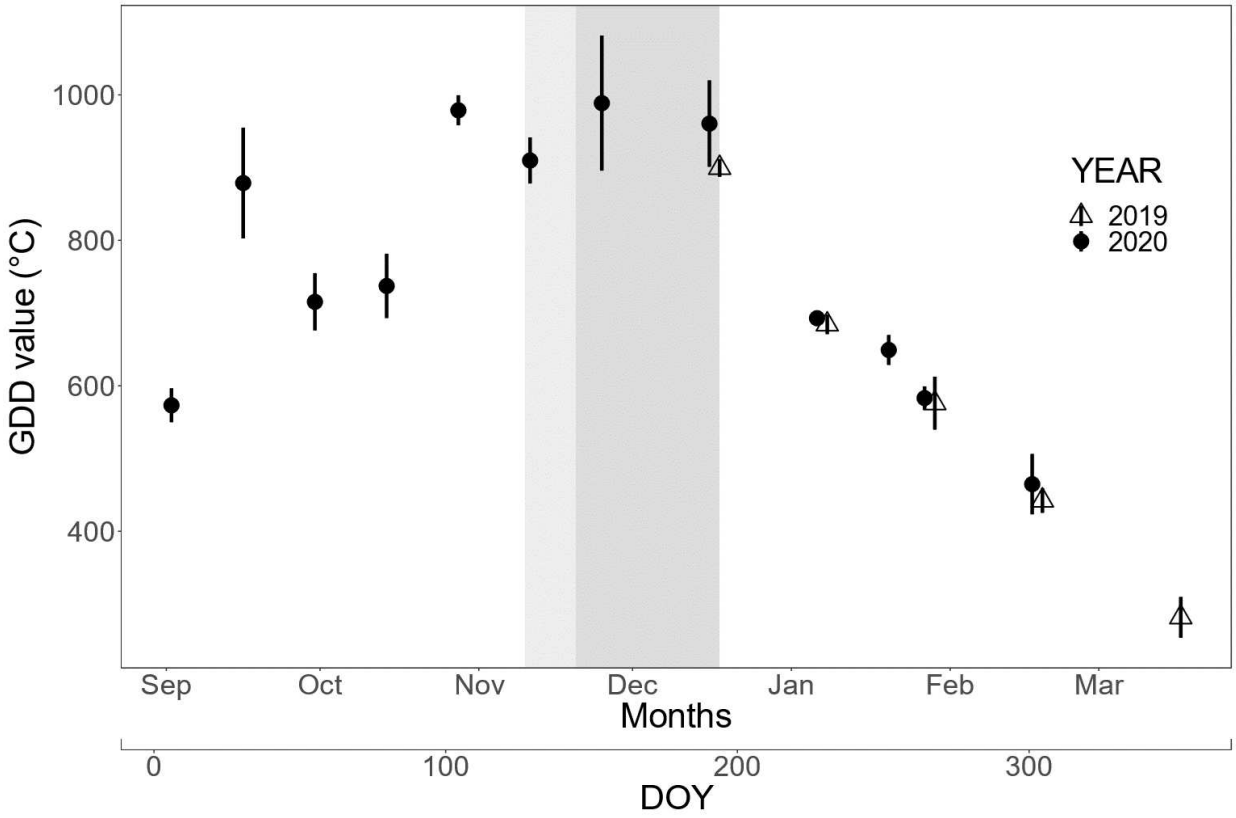

Figure 3: Dormancy depth in September – March for potted young trees in outside ambient conditions. Growing degree days (GDD, °C) needed to break the dormancy of trees grown at ambient temperature outside and placed in growth chambers at 22°C and 16 h light. Means are represented by triangles for December 2019 to March 2020 and circles for September 2020 to February 2021 (± SE, n=3). Dark grey represents the warming period for Exp 1, while light grey represents the warming period for Exp 2.

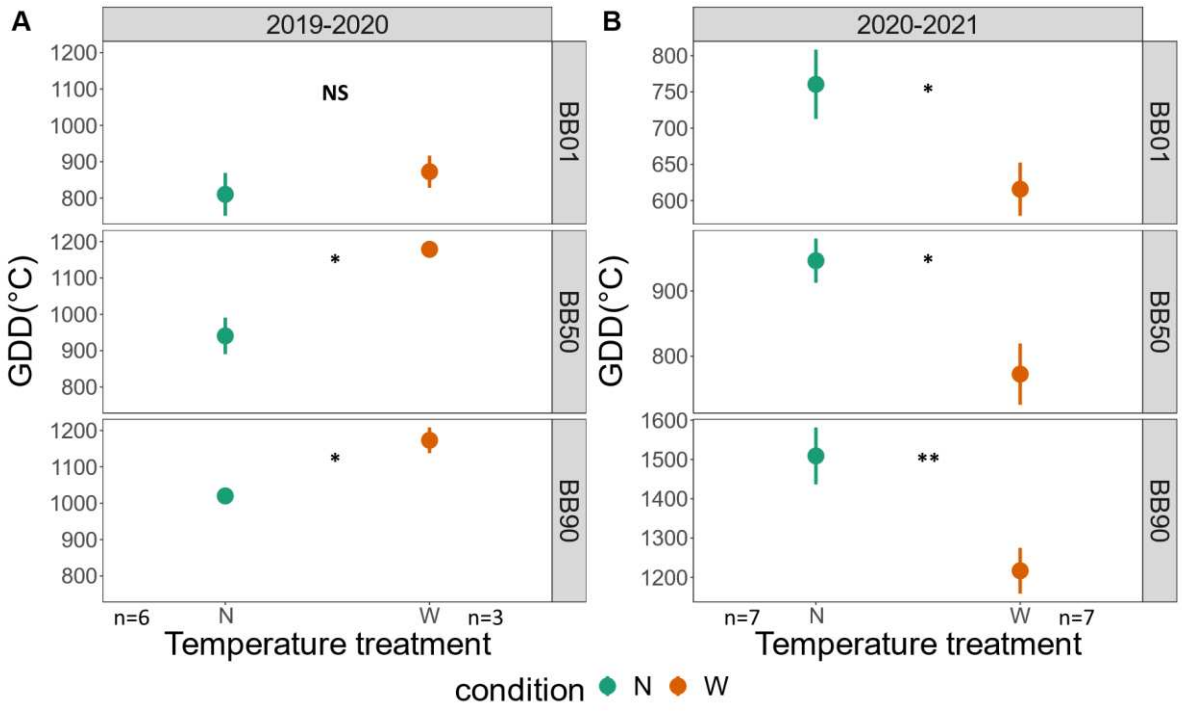

Figure 4: Dormancy depth after temperature treatment. Bud dormancy depth after temperature treatments (N: normal ambient temperature; W: warming temperature) in the 2019-2020 (A) and in the 2020-2021 (B) experiments. The dormancy depth was measured as the heat (growing degree days or GDD, in °C) needed to open the first bud (BB01), 50% of the buds (BB50) and 90% of the buds (BB90). Statistics: NS : non-significant ($p>0.05$); * : $p\leq0.05$, and ** : $p\leq0.01$. The number of replicates (n) is also reported at the bottom.

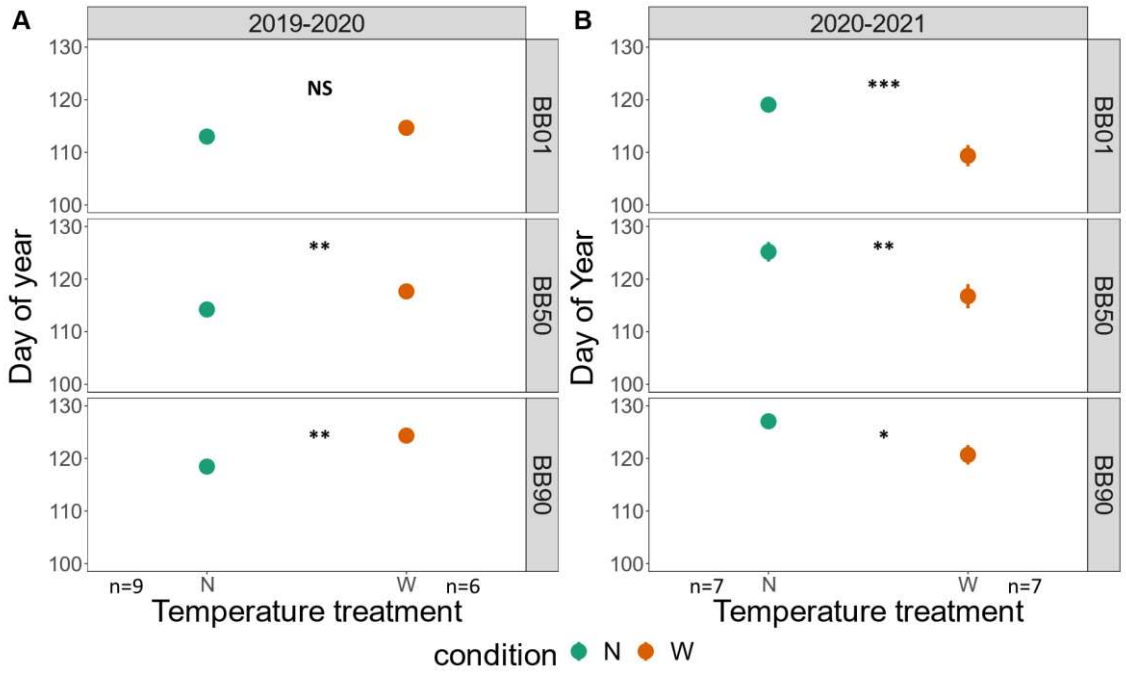

Figure 5: Spring budburst after temperature treatment. Spring budburst after the temperature treatment (N: normal ambient temperature; W: warming temperature) in the 2019-2020 (A) and in the 2020-2021 (B) experiments. BB01 represents the date when the first bud was opened, BB50 when 50% of buds were opened and BB90 when 90% of buds were opened. Statistics: NS: non-significant ($p>0.05$); *: $p\leq0.05$; **: $p\leq0.01$, and *** $p\leq0.001$. The number of replicates (n) is also reported at the bottom.

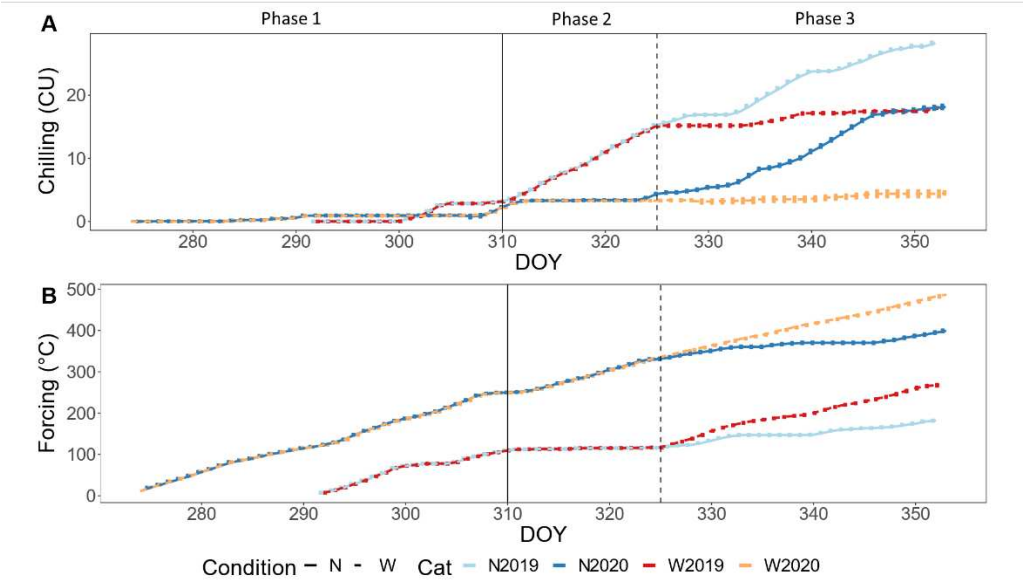

Figure 6: Forcing and chilling from the senescence onset until the end of the experiment. Chilling (A) and forcing (B) accumulation from senescence onset until the end of the warming experiment determined with the Sequential Model. The blue lines represent normal ambient temperature treatment (N), for 2019 (light blue) and 2020 (dark blue). Warming treatments (W) are shown in dashed red (2019) and dashed orange (2020). The warming took place between 20/11/2019 (DOY 324) and 18/12/2019 (DOY 352) in the 2019 experiment and between 10/11/2020 (DOY 314) and 18/12/2020 (DOY 353) in the 2020 experiment. The study period has been divided into three phases: (1) from onset of senescence till DOY 310 (black vertical line); (2) from DOY 311 till DOY 325 (black vertical dashed line) and (3) from DOY 326 till 353.

Supplemental data

Table 1 S1: Average, minimum and maximum daily temperature during the months of October till March of 2019 – 2020 and 2020-2021.

Year	Month	Exp	mean (°C)	min (°C)	max (°C)
2019	October	exp1	12.3	8.9	17.6
2019	November	exp1	6.5	2.9	11.8
2019	December	exp1	5.8	2.7	9.5
2020	January	exp1	6.2	3.5	9.5
2020	February	exp1	7.3	3.7	11.6
2020	March	exp1	7.5	3.0	13.1
2020	October	exp2	11.8	8.5	16.5
2020	November	exp2	9.1	5.3	14.3
2020	December	exp2	5.8	3.2	8.9
2021	January	exp2	3.6	1.1	7.1
2021	February	exp2	5.2	1.3	10.1
2021	March	exp2	7.6	2.8	13.0

Table S2: Senescence onset date: This table reports the average date of senescence onset (DOY) determined from data of single tree chlorophyll content index (CCI) or aggregated data of CCI for all trees, for 2019 and 2020.

	Senescence onset ± SD	
	Mean of single tree data with interindividual uncertainty	**Aggregated data with method uncertainty**
2019	292 ±11.3	292 ± 4.3
2020	274 ±16.7	277 ±2.7

Table S3: Comparison of chilling models with different parameterizations. Model results obtained from the standard model parameterization of Sequential Model and Unified Model used in the main analysis and from alternative parametrizations for trees under warming (W) and normal temperature treatment (N).

	Chilling units for N		Chilling unit for W		Simulation period	parameterization species	Reference parameterization
	2019	2020	2019	2020			
Sequential model							
Version reported in main text	28	18	18	5	1/11 to 31/12	*Fagus sylvatica L.*	Fu et al., 2012b
Version Gala	43	34	32	22	1/11 to 31/12	*Malus domestica Borkh*	Pertille et al., 2019 Guak and Neilsen, 2013
Version Cherry	49	39	37	25	1/11 to 31/12	*Prunus avium L.*	Guak and Neilsen, 2013 Pertille et al., 2019
Unified model							
Version reported in main text	73	70	70	66	1/09 to 31/12	*Juglans regia L.*	Chuine et al., 2016; Pertille et al., 2019
Version apricot (calibrated against dormancy depth)	66	63	62	58	1/09 to 31/12	*Prunus armeniaca L.*	Chuine et al., 2016; Pertille et al., 2019
Version willow (not calibrated against dormancy depth)	49	29	31	13	1/09 to 31/12	*Salix matsudana*	Pertille et al., 2019; Xu and Chen, 2013

Table S4: Statistical result of the impact of warming on dormancy depth and spring budburst when using different approaches. Statistical significance value (p) of the warming on dormancy depth and spring bud-burst for Exp2 when considering (in mixed models) or not (in ANOVA analysis) the random effect of greenhouse unit.

	Mixed models		ANOVA analysis	
	Dormancy depth	**Spring bud-burst**	**Dormancy depth**	**Spring bud-burst**
BB01	0.01	0.04	0.03	0.0006
BB50	0.01	0.01	0.02	0.008
BB90	0.01	0.04	0.008	0.01

Table S5: Observational date of spring budburst per experimental year and temperature treatments. W: warm temperature treatment, N: normal ambient temperature treatment, and "outside" as untreated trees kept always outside.

Year	Condition	OBERVATION (BB01)	
		DOY	SE
2020	**N**	113	0.3
2020	**W**	115	1.0
2020	**outside**	112	0.3
2021	**N**	123	0.7
2021	**W**	109	2.0
2021	**outside**	119	0.4

Table S6: Chilling and forcing accumulation from senescence until budburst. Chilling and forcing for four different phases: (1) from onset of senescence till beginning November (DOY 310); (2) from beginning till end of November (DOY 311-325); (3) from end November till end of the experimental warming (DOY 326-353) and (4) from the end of temperature treatment until end of May. The total accumulation represents the accumulation from phase 1 to phase 4.

	Chilling 2019 (CU)		Chilling 2020 (CU)		Forcing 2019 (°C)		Forcing 2020 (°C)	
	N	**W**	**N**	**W**	**N**	**W**	**N**	**W**
Phase 1	3	3	2	2	110	110	250	250
Phase 2	12	12	2	1	7	7	77	86
Phase 3	13	3	15	0	65	151	67	155
Phase 4	57	57	74	74	726	726	471	471
Total Accumulation	85	75	93	77	908	993	865	962

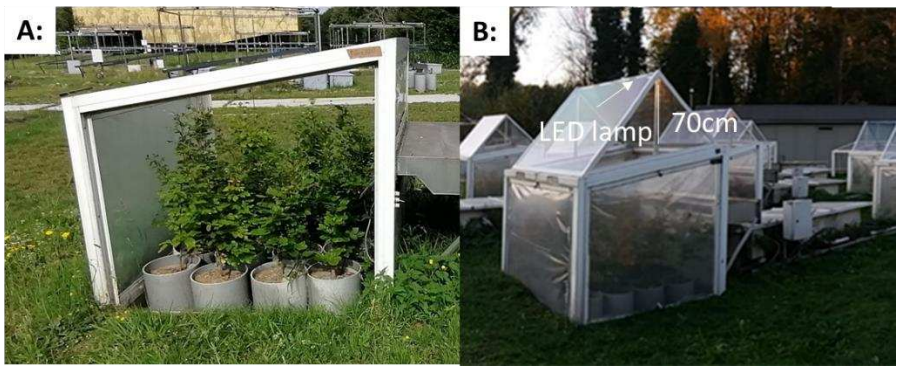

Figure S1: Climate controlled greenhouses. A: set-up used during experiment 1 in winter 2019 - 2020; B: set up used during experiment 2 in winter 2020- 2021.

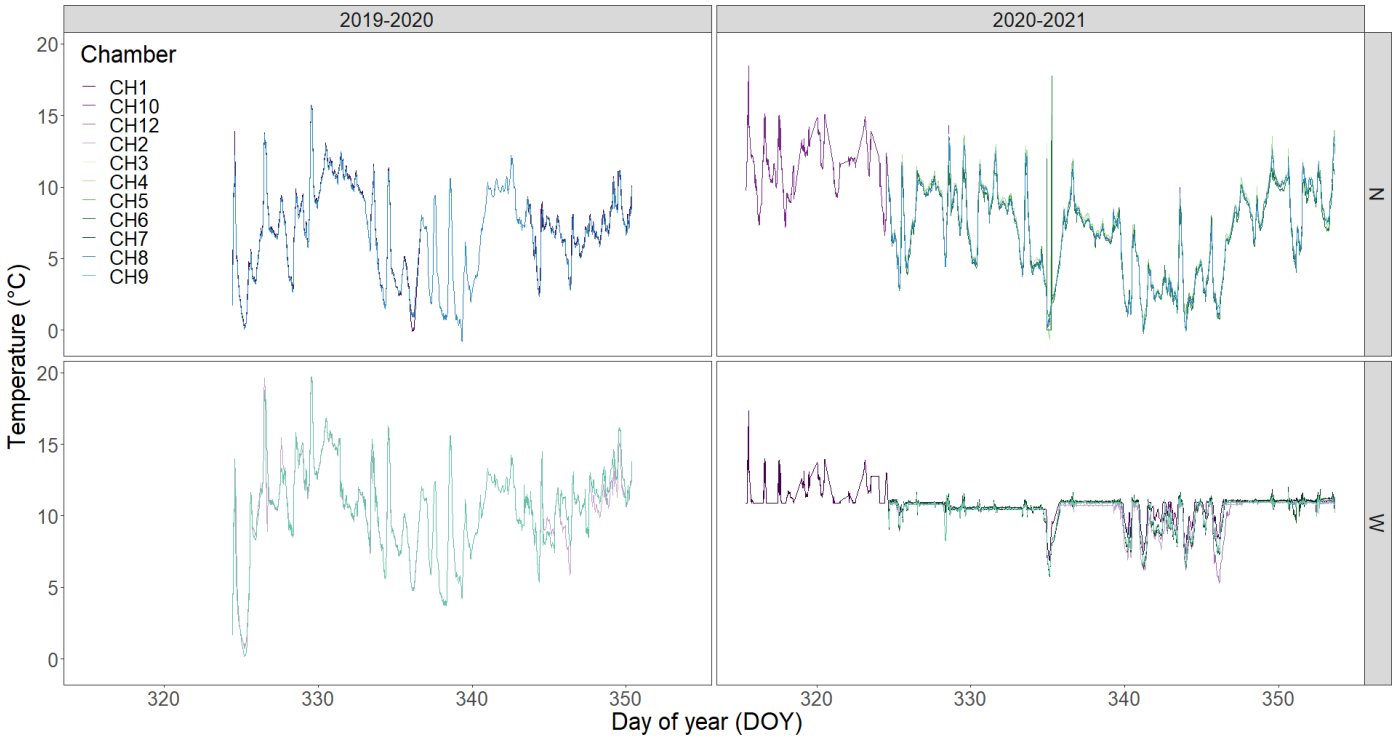

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Figure S2: Temperature data per greenhouse. Each greenhouse in the same temperature treatment followed the same 766

temperate pattern. W: trees under warming treatment; N: trees under normal ambient temperature treatment. 767

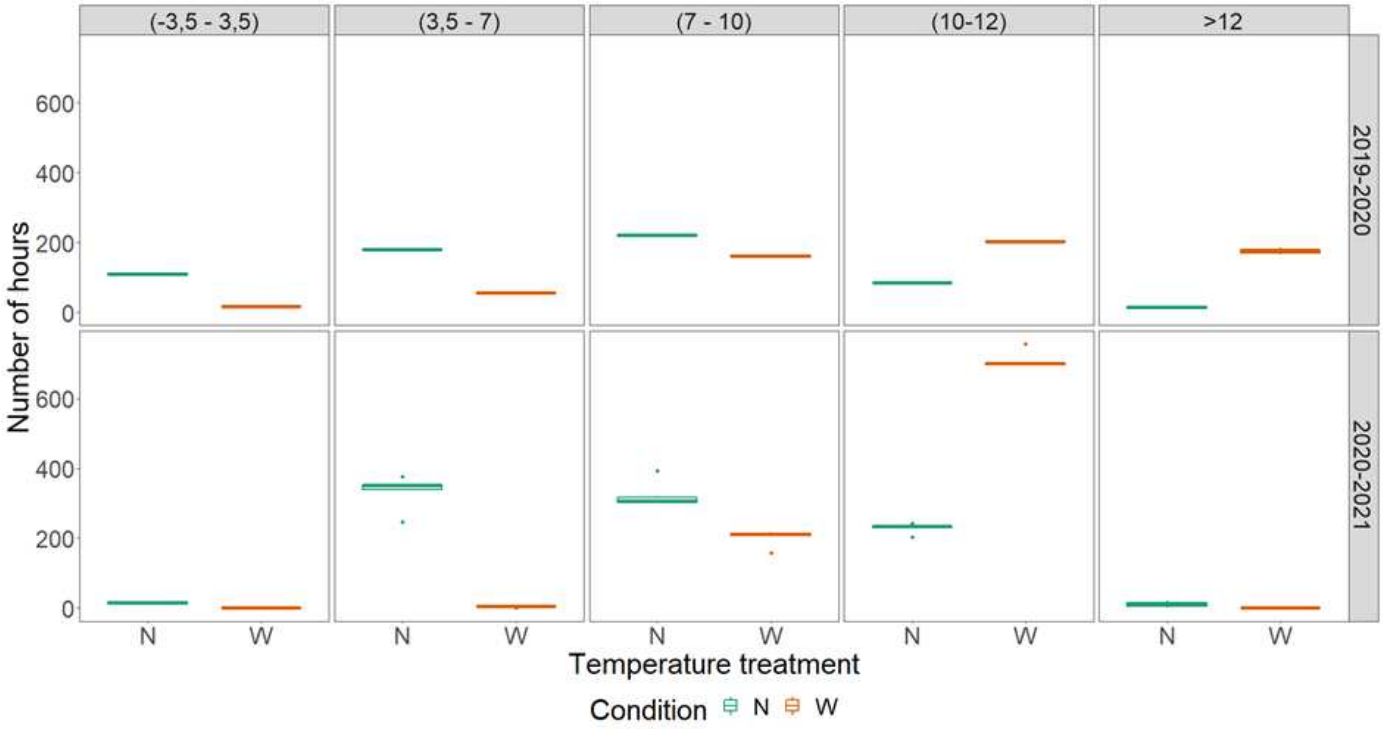

Figure S3: Chilling hours per temperature range. In 2019-2020 we applied a warming treatment of 613h and in 2020-2021 a warming treatment of 916h. This graph represents the timing in hours per temperature range. In orange, we represented the warming temperature treatment (W) and in green the normal temperature treatment (N). The mean temperature per hours between -3.5 and 3.5°C, between 3.5 and 7°C, between 7 and 10°C, between 10 and 12 °C, and >12°C, is represented by thick lines with vertical bars indicating their uncertainty (± SE). For each specific temperature range, numbers of hours are always significantly different between W and N at $p<0.01$.

Species	0	1	2	3	4
Fagus sylvatica					
Information	Dormant buds	Swollen buds	Opening of buds = budburst	Leave are emerging	Leaves are completely out

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Figure S4: Bud development scale. Bud developmental stages of *Fagus sylvatica L.*, based on Davi et al., 2011. Stage 2 is 778

considered as budburst. 779

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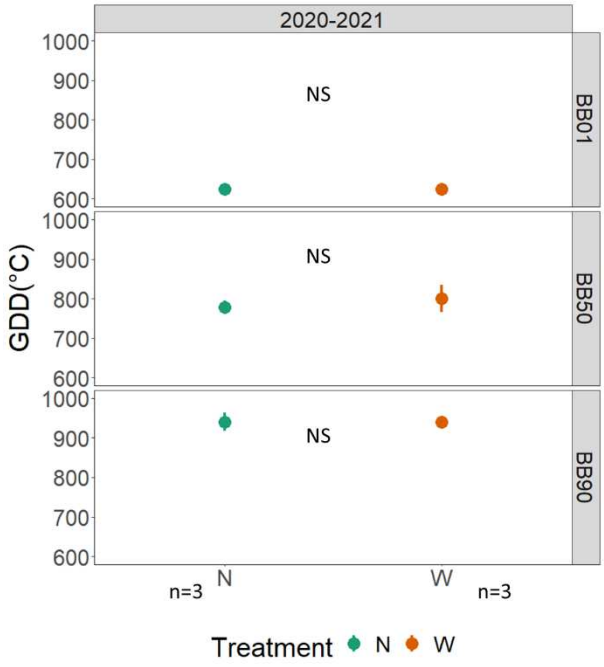

Figure S5: Bud dormancy before the temperature treatment. This graph represents the bud dormancy before the temperature treatment measured as GDD (°C) needed to open the first bud (BB01), 50% of the buds (BB50) and 90% of the buds (BB90) in 2020-2021. W indicates trees that were subsequently used for high temperature treatment, while N trees that were subsequently used for normal ambient temperature treatment. No significant difference was recorded between pairs of tree groups (test done was ANOVA n=3, $p>0.5$).

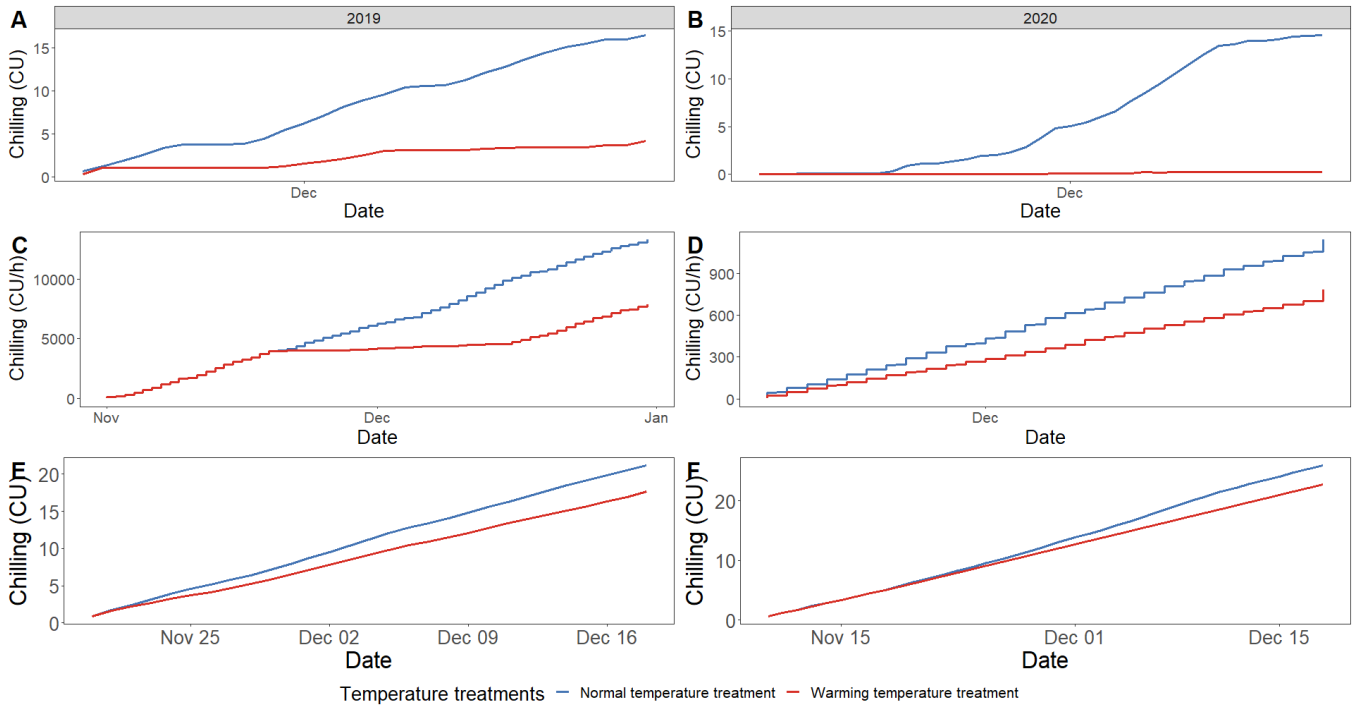

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Figure S6: **Chilling simulations**. Chilling calculation based on SM (A, B), Utah model (C,D) and UM (E,F) for 2019-2020 790

and 2020-2021 respectively. In red warmed temperature treatment and in blue normal temperature treatment. 791

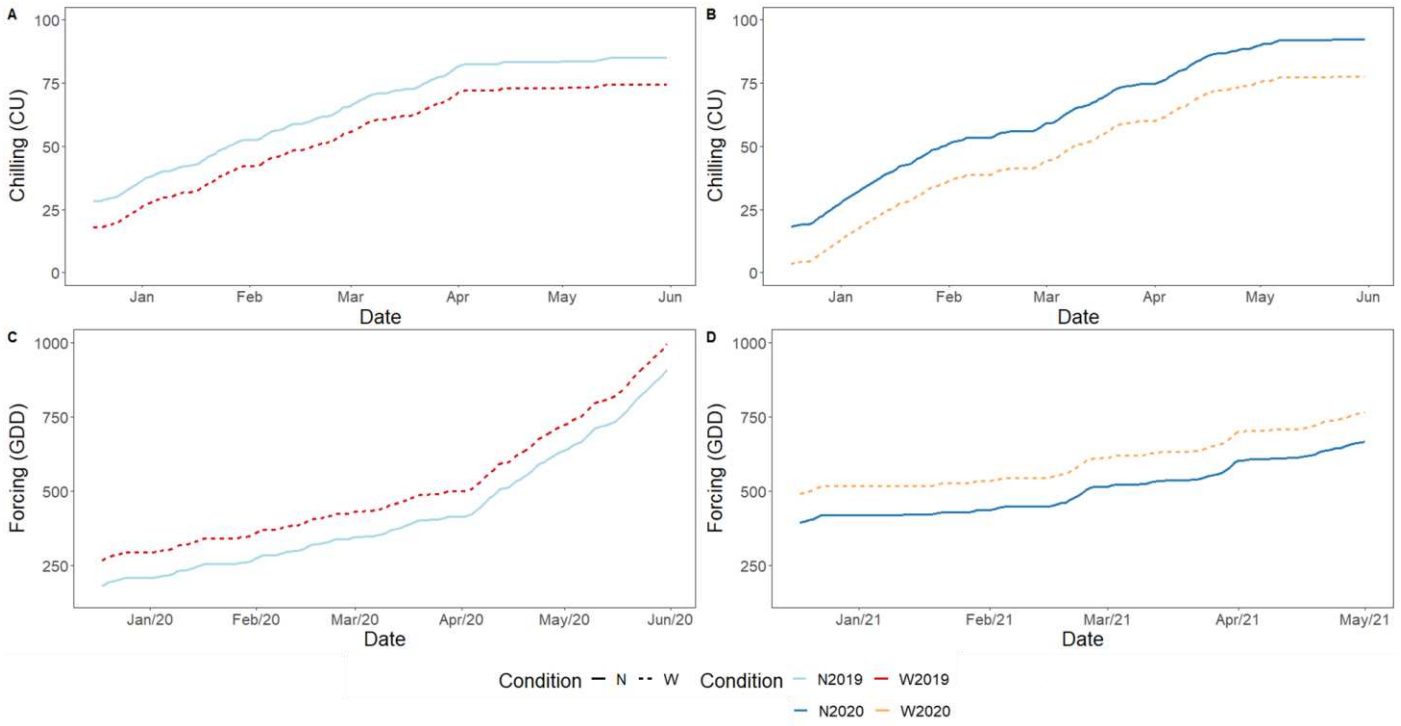

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Figure S7: Chilling and forcing from 18/12 to end of May: Calculation based on SM model for Exp1 (A and C) and 793

Exp2 (B and D) for chilling and forcing. Warming treatments (W) are in dashed red (2019) and dashed orange (2020). 794

The study period correspond to the phase 4 (from 18/12 until 31/05). 795

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REFERENCE

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. Glob. Change Biol. 22, 3444–3460. https://doi.org/10.1111/gcb.13383

Davi, H., Gillmann, M., Ibanez, T., Cailleret, M., Bontemps, A., Fady, B., Lefèvre, F., 2011. Diversity of leaf unfolding dynamics among tree species: New insights from a study along an altitudinal gradient. Agric. For. Meteorol. 151, 1504–1513. https://doi.org/10.1016/j.agrformet.2011.06.008

Fu, Y.H., Campioli, M., Van Oijen, M., Deckmyn, G., Janssens, I.A., 2012. Bayesian comparison of six different temperature-based budburst models for four temperate tree species. Ecol. Model. 230, 92–100. https://doi.org/10.1016/j.ecolmodel.2012.01.010

Guak, S., Neilsen, D., 2013. Chill unit models for predicting dormancy completion of floral buds in apple and sweet cherry. Hortic. Environ. Biotechnol. 54, 29–36. https://doi.org/10.1007/s13580-013-0140-9

Pertille, R.H., Sachet, M.R., Guerrezi, M.T., Citadin, I., 2019. An R package to quantify different chilling and heat models for temperate fruit trees. Comput. Electron. Agric. 167, 105067. https://doi.org/10.1016/j.compag.2019.105067

Xu, L., Chen, X., 2013. Regional unified model-based leaf unfolding prediction from 1960 to 2009 across northern China. Glob. Change Biol. 19, 1275–1284. https://doi.org/10.1111/gcb.12095