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Climate change and shifts in dormancy release for deciduous fruit crops in Germany

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ABSTRACT: Four different chilling models, the Weinberger-Eggert model (C1), Utah model (C2), Positive Utah model (C3), and Dynamic model (C4), were used to evaluate possible future changes in the date of dormancy release (t_1) in Germany for deciduous fruit crops with a chilling requirement (C*) ranging from 700 to 1800 chill units. The study was based on gridded air temperature data in a 7 × 11 km horizontal resolution for current and future climate conditions. Currently, dormancy of low chill crops, up to ~1000 chill units, is released evenly across Germany. However, for high chill cultivars (1500 to 1800 chill units) the chilling fulfillment occurs later in the colder continental, SE areas than in the mild, maritime NW regions of Germany. For future climate conditions (2071 to 2100), the patterns of t_1 will change, depending on the regional temperature rise. As a result, the areas which currently have a late date of dormancy release could have an advanced date in the future and vice versa, reducing the current differences between the northern and southern areas. Among the models, we found some different results. Model C1 showed a delay of t_1 for all values of C*. The other chilling models (C2–C4), showed a delay in t_1 for low chill varieties (700 to 1000 chill units), only small changes for medium chill varieties (1100 to 1400 chill units), and an earlier timing in the end of winter dormancy for fruit crops with a high C* (1500 to 1800 chill units). If we follow the results of these 3 models, we conclude that dormancy in a wide range of deciduous fruit crops in Germany will be released early enough to ensure a timely start of reproductive development in the future.

KEY WORDS: Chilling requirement · Chilling models · Climate change · Germany

1. INTRODUCTION

Winter dormancy in temperate zones is necessary to avoid damages to woody plants due to unfavourable climatic conditions (e.g. Saure 1985, Lang 1994, Faust et al. 1997, Arora et al. 2003, Campoy et al. 2011). Generally, we have to distinguish 3 types of dormancy (Lang et al. 1987). The first type, *paradormancy* is initiated in late summer by environmental triggers (e.g. changes in daylength or temperature) or by the correlative inhibition of growth among different parts of the plant (apical dominance). The genuine dormancy, on which we focus in this paper, is called *endodormancy* (winter dormancy). It is also induced by changes in environmental conditions (e.g. decreasing temperatures, photoperiod, and changes in light spectrum) and is later controlled by phytohormones in plant tissue. A certain period of low temperatures (plant specific C*) is necessary to repeal that state. This process can be described by different chilling models (see Section 2.1.). *Ecodormancy* (quiescence) follows endodormancy and is the inhibition of growth due to limiting environmental conditions, such as low temperatures in winter or early spring. Plants are released from ecodormancy by favourable environmental conditions that promote the development of vegetative and generative organs.

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A precondition for the successful growing of deciduous fruit crops is that the C* of the crop must be fulfilled (Coville 1920). In temperate zones (40 to 60° N) winter chilling was not an important issue in the past, because the temperatures between autumn and spring were always low enough to satisfy the C* of deciduous fruit crops. In tropical and subtropical regions (e.g. Israel, California, and South Africa), it is rather difficult to grow all kinds of temperate fruit, because in these regions winter chill is already limited today. Here the question 'Is it a good chilling year?' is common (Niederholzer 2009). Insufficient chilling can lead to a delayed or irregular budburst and beginning of blossom, or to a lower blossoming rate and higher bud drop (Legave et al. 1982, Erez 2000).

Climate change can also influence the timing of winter dormancy release in temperate regions. For Germany, the strongest temperature rise (REMO-UBA, A1B, 2071–2100 minus C20, 1971–2000) is expected for winter (+3.9 ± 2.1°C, mean ± SD), followed by autumn (+3.5 ± 1.3°C), summer (+3.2 ± 1.7°C) and spring (1.8 ± 1.7°C), (Chmielewski et al. 2009). Rising temperatures between autumn and spring can lead to either an earlier or a later chilling fulfillment, depending on current temperatures, and consequently to shifts in the beginning of bud burst, leaf unfolding, and blossom. For this reason, phenological modellers have to consider the date of dormancy release in combined chilling/forcing models (Chuine et al. 1999, 2003, Chmielewski et al. 2011, Matzneller et al. 2012). A lack of chilling can only be partially compensated by a higher forcing rate of the trees (Murray et al. 1989).

Most fruit crops in Germany show an earlier beginning of blossoming since the end of the 1980s (Chmielewski et al. 2004, Estrella et al. 2007, Blanke & Kunz 2009); early blossoming species such as apricot and peach advanced by 15 d or more between 1961 and 2005 (Chmielewski 2012). In contrast, for the Tibetan Plateau a delay in spring phenology was reported by Yu et al. (2010), which could already be the result of late or insufficient chilling in the warm period 1982–2006. For some subtropical regions, decreases in winter chill are being observed. For instance, for high-elevation oases in Oman, an average decrease of 1.2 to 9.5 chilling hours (CH) yr^{-1} between 1983 and 2008 has been detected (Luedeling et al. 2009b). The authors concluded that climate change can limit the cultivation of traditional fruit trees in these regions. Similar results were achieved for growing regions in California (Baldocchi & Wong 2008, Luedeling et al. 2009c,d,e). While notable, long-term declines in winter chill accumulation were found for some fruit growing regions in Australia, no trends were detected at other sites (Darbyshire et al. 2011). For the western USA, Schwarz & Hanes (2010) found trends towards less chilling in Washington State, California, and Arizona, and more chilling in interior regions. For the whole of Germany no significant temporal trend in winter chill between 1950 and 2010 was found (Luedeling et al. 2009a). Additionally, the regional trends depended on the choice of chilling model.

C* varies in wide ranges among the fruit crops and within the varieties (Baldocchi & Wong 2008). The C* for European apple, pear and plum lies between 800 and 1800 CH. Cherries require ~700 to 1300 CH. Some subtropical varieties have a lower C*.

We calculated the dates of dormancy release for Germany, depending on the C* of the fruit crop (700–1800 CH) for current (1971–2000) and for future climate conditions (REMO-UBA, scenario A1B, 2071–2100), using 4 chilling models developed on the basis of field observations and data derived under controlled climate conditions. Even if it is not possible to validate the models on observational data, because the end of winter dormancy cannot be observed with accuracy, it is possible to derive conclusions on the applicability of the models for current and future climate conditions (Anderson & Seeley 1992).

2. MATERIALS AND METHODS

2.1. Chilling models

In chilling models, the state of chilling $S_c(t)$ is usually the sum over the chilling rate function between t_0 (the beginning of chilling accumulation in autumn) and t_1, the date when the plant is released from endodormancy. R_c is the chilling rate for a single time step (Eq. 1):

$$S_c\left(t\right) = \sum_{i=t_0}^{t} \sum_{h=1}^{24} R_c\left(T_{ih}\right) \qquad (1)$$

Altogether, 4 different chilling models (C1 to C4) were tested.

2.1.1. C1: Weinberger-Eggert model

Also called the Chilling Hour model (Weinberger 1950), this was originally developed to describe the rest breaking of 2 peach cultivars *Prunus persica* (L.)

in Georgia. It accumulates chilling hours (CH) between 0 and 7.2°C:

$$R_c(T_{ih}) = \begin{cases} 1\text{ CH if } 0\text{ °C} < T_{ih} < 7.2\text{ °C} \\ 0\text{ CH if } T_{ih} \le 0\text{ °C or } T_{ih} \ge 7.2\text{ °C} \end{cases} \quad (2)$$

All hours with temperatures in this range count for 1 CH. This is a limitation of the model, because in reality there is an optimal temperature that contributes most strongly to the rest completion (e.g. Erez & Lavee 1971, Anderson & Seeley 1992). Weinberger (1967) itself stated that the chilling effect can be reversed by high winter temperatures. Despite these limitations, the CH model is well known among the farmers and frequently used to describe the C* of fruit crops, probably because of the ease of calculation.

2.1.2. C2: Utah model

This model (Richardson et al. 1974) uses weighted chilling hours, termed chill units (CU). It considers only positive hourly temperatures, but with an optimal chilling effect between ≥2.5 and <9.2°C:

$$R_c(T_{ih}) = \begin{cases} 0.0\text{ CU if } T_{ih} < 1.5\text{ °C} \\ 0.5\text{ CU if } 1.5\text{ °C} \le T_{ih} < 2.5\text{ °C} \\ 1.0\text{ CU if } 2.5\text{ °C} \le T_{ih} < 9.2\text{ °C} \\ 0.5\text{ CU if } 9.2\text{ °C} \le T_{ih} < 12.5\text{ °C} \\ 0.0\text{ CU if } 12.5\text{ °C} \le T_{ih} < 16.0\text{ °C} \\ -0.5\text{ CU if } 16.0\text{ °C} \le T_{ih} < 18.0\text{ °C} \\ -1.0\text{ CU if } T_{ih} \ge 18.0\text{ °C} \end{cases} \quad (3)$$

Temperatures in this range count for 1 CU (or Utah Chilling Units, UCU), while temperatures below or above this range have smaller weights. Temperatures between ≥12.5 and <16°C do not count, and higher temperatures count as negative chilling units. The model works well in continental climates with cold winters, but it can fail in subtropical climates (del Real-Laborde 1987, Dennis 2003, Luedeling & Brown 2011), because the accumulation of negative chill units is too high.

2.1.3. C3: Modified Utah model

This version omits the negative temperature range of C2 and can be used in subtropical climates. The temperature ranges in this Positive Utah model (Linsley-Noakes et al. 1995) are identical to the C2 model, but only hourly temperatures between ≥1.5 and <12.5°C are relevant:

$$R_c(T_{ih}) = \begin{cases} 0.0\text{ CU if } T_{ih} < 1.5\text{ °C} \\ 0.5\text{ CU if } 1.5\text{ °C} \le T_{ih} < 2.5\text{ °C} \\ 1.0\text{ CU if } 2.5\text{ °C} \le T_{ih} < 9.2\text{ °C} \\ 0.5\text{ CU if } 9.2\text{ °C} \le T_{ih} < 12.5\text{ °C} \\ 0.0\text{ CU if } T_{ih} \ge 12.5\text{ °C} \end{cases} \quad (4)$$

The model calculates Positive Chilling Units (PCU).

2.1.4. C4: Dynamic model

This model (Fishman et al. 1987a,b) considers the dynamic of hourly temperatures on rest release. It is similar to the Utah model (bell shape dependence on temperature for rest completion between –2 and 13°C, and negation of the chilling effect by high temperatures), but it adds physiological meaning on the basis of experiments (Couvillon & Erez 1985, Erez & Couvillon 1987), and considers the length of a temperature cycle during rest completion. When plants are exposed to high temperatures only for a short time in a daily cycle (e.g. a few hours with temperatures >18°C), the chilling effect is enhanced, while long exposures to high temperature lead to chilling negation (Fishman et al. 1987a). Additionally, a short exposure of the buds to moderate temperatures (13 to 16°C) in a daily cycle with lower temperatures can enhance rest completion. The model assumes that the degree of dormancy completion depends on dormancy-breaking factors, which accumulate in buds in a 2-step process (Linsley-Noakes & Allan 1994). The first step is assumed to be a reversible process that produces a thermally labile precursor (Eq. 5):

$$x(t) = x_s - \left[x_s - x(t-1)\right]\mathrm{e}^{-k_1} \quad (5)$$

Formation of the precursor is promoted by chilling temperatures between 0 and 12°C with an optimum between 6 and 8°C, while higher temperatures reverse this process. Temperatures between 13 and 16°C can also enhance the process if they are cycled with lower temperatures. Once a critical portion (CP) of the precursor is accumulated $x(t) \ge 1$, it is transformed irreversibly in the second step, to one portion of a stable dormancy-breaking factor or chill portion (Eq. 6):

$$\text{If } (x(t) \ge 1)\text{, then } \begin{cases} delt = x(t) \cdot P_t \\ \mathrm{CP} = \mathrm{CP} + delt \\ x(t) = x(t) - delt \end{cases} \quad (6)$$

The steady-state value (x_s), rate constant (k_1), and transition probability (P_t) are functions of the temperature T_{ih} and depend on 6 constants (A_0, A_1, E_0, E_1, c, d; see Fishman et al. 1987a,b). 'delt' is the amount of chilling portions which was accumulated in the first step (unstable precursor portions) and now is transformed to the accumulated, stable chill portions. The model starts with $x(t = 1) = 0$ and CP = 0. t_1 is defined as the time t when the accumulated chill portions are $\geq C^*$ for the first time (see Fishman et al. 1987b, Erez et al. 1988, Erez & Fishman 1998).

2.1.5. Model intercomparison

Models C3 and C4 work well in cold and warm climates, while C4 is probably the best model to describe dormancy release in subtropical zones (Erez et al. 1990).

One CP equals 28 h at 6°C, but only if the temperature stays constant for this time period (Erez & Fishmann 1998). Thus, it is generally difficult to translate CP into other units such as CH or CU (Luedeling & Brown 2011, Campoy et al. 2012). Erez et al. (1990) used a ratio of 1:20 to compare UCU with CP graphically. According to Niederholzer (2009), 95 CP may 'equal' 1500 CH, a ratio of 1:16. For Germany we found by linear regression an average ratio of 1:18; therefore, we multiplied the chill portions by 18 to compare them to chilling hours: x CP = (x·18) (CP/18).

The models were started on 1 September ($t_0 = 244$ day of year, DOY), because August temperatures are usually too high to initiate chilling. Models C1 and C3 accumulate positive chilling hours directly after 1 September if optimal chilling temperatures occur. Model C2 first starts to sum negative chilling units, since the temperatures in September are usually not low enough ($T_{ih} < 12.5$°C, Eq. 3) to enable a continuous positive chilling accumulation. This behaviour of Model C2 was used to determine the starting date of chilling hour accumulation. It was the date after 1 September when the lowest negative chilling sum was reached. Model C4 also uses a self-regulating beginning of chilling accumulation, which starts if the first chill portion (Eq. 6) is permanently fixed (Cesaraccio et al. 2004). For all models the calculation was not stopped before a specified value of C^* was reached. This final date was the date of dormancy release (t_1).

2.2. Temperature data

Daily air temperature data (T, T_x, T_n) from the German Meteorological Service (DWD) between 1971 and 2000 was used (523 stations across Germany). The station data were attributed to a 7 × 11 km grid (0.1° resolution), using second order universal kriging with implicit height regression (Wackernagel 1998, Blümel & Chmielewski 2011). As a result, daily data of air temperatures from 4 253 grid points (GP) in the period 1971–2000 were available to calculate the release of dormancy across Germany for chilling requirements between 700 and 1800 chill units. Through the use of gridded data, we were able to cover all of Germany with temperature data, gaps in the time-series of individual stations were not an issue, and we were able to compare the results derived from a climate scenario (always gridded data) with the observations in the same spatial resolution and at the same grid points. A disadvantage of the dataset could be that local temperature features of river valleys or terraced slopes, which could be important in some orchard regions, are not well represented in this record. In a small-scale analysis, such local features would be important.

We used the regional climate model REMO-UBA to investigate how the release of dormancy may change in the future (Jacob et al. 2001). REMO is a 3-dimensional hydrostatic model developed by the Max-Planck Institut für Meteorologie and Deutsches Klimarechenzentrum on behalf of the Federal Environmental Agency (UBA). The REMO is driven by the global circulation model ECHAM5/MPI-OM (Roeckner et al. 1996, 2003). The model area of REMO-UBA includes Germany, Austria and Switzerland with a horizontal resolution of 0.1°.

We investigated possible changes according to the IPCC (2007) emission scenario A1B only. For the control run (C20), the years between 1971 and 2000 were chosen. The scenario data covered the period 2011–2100. The spatial resolution of the RCM data was the same as that of the observations.

We generated hourly temperatures, which are necessary to run chilling models, from daily data by the following equations (Linsley-Noakes et al. 1995):

$$\text{Day}: T_h = (T_x - T_n) \cdot \sin\left(\frac{\pi \cdot t}{DL + 4}\right) + T_n \tag{7}$$

$$\text{Night}: T_h = T_{ss} - \frac{T_{ss} - T_n}{\ln(24 - DL)} \cdot \ln(t) \tag{8}$$

where T_h is the temperature at t hours after sunrise ($t \geq 0$), or at t hours after sunset ($t \geq 1$), respectively. T_x is the daily maximum, T_n the daily minimum, T the daily mean temperature, DL the daylength in h, and T_{ss} the temperature at sunset, as obtained from the daytime solar cycle in Eq. (7).

These calculations are also possible on the basis of hourly data, directly derived from the observations

(DWD) or the REMO-UBA model (C20, A1B), although this increases computing time. It would also be difficult to obtain hourly temperatures for all 523 weather stations for 1971–2000. For this reason we compared the calculations of t_1 on the basis of real hourly and daily data (in this case, hourly data were generated from the daily extreme temperatures according to Eqs. 7 & 8) only for the region of Hessen (81 grid points). Fig. 1 shows the end of dormancy release (t_1) according to Models C1 and C3 for a C* between 700 and 1800 CH/PCU in Hessen for the C20 (1971–2000) and A1B (2071–2100) model run. The timing of dormancy release between both methods never differed by >5 d, and we decided to use computational daily temperature data for the entire study. We also found that the observed daily temperature cycle was well approximated by the equations from Linsley-Noakes et al. (1995).

2.3. 'Delta change' approach

The 'delta change' approach (Andreasson et al. 2004) can be used to compare results derived from an

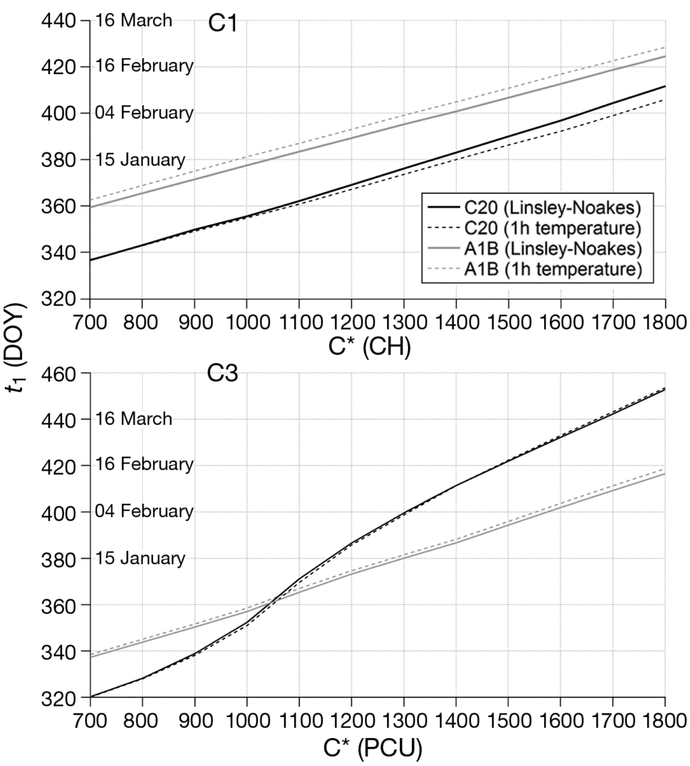

Fig. 1. Average date of dormancy release (t_1) in Hessen for different chilling requirements (C*) (REMO-UBA: C20, 1971–2000; A1B, 2071–2100) by using real hourly data (1 h temperature) from the RCM and generated hourly data (Linsley-Noakes), see Eqs. (7) & (8)

RCM, with observations, if the climate model is not corrected for bias. In our study, the date of dormancy release (t_1) was calculated on the basis of the gridded temperature data for 1971–2000 (DWD observations). In the RCM, the current climate is represented by the control run (C20). We calculate future changes in dormancy release ($\Delta\overline{t_1}$) by differences between the climate scenario (A1B, 2071–2100) and the control run (C20, 1971–2000). Changes of $\overline{t_1}$ at the end of this century are calculated as follows:

$$\Delta\bar{t}_1\left(\text{A1B-C20}\right) = \bar{t}_1(\text{A1B})^{2071-2100} - \bar{t}_1(\text{C20})^{1971-2000} \quad (9)$$

To compare possible future dates of dormancy release derived from the RCM with the current dates calculated from observations, the changes in the model $\Delta\overline{t_1}$ according to Eq. (9) were added to the calculated dates of $\overline{t_1}$ for the current climate (1971–2000):

$$\bar{t}_1^{2071-2100} = \bar{t}_1(\text{DWD})^{1971-2000} + \Delta\bar{t}_1\left(\text{A1B-C20}\right) \quad (10)$$

We used this method in Fig. 7 to present mean values of dormancy release for 2071–2100.

3. RESULTS

3.1. Dormancy release for current climate conditions

Cultivars with a chilling requirement up to 1800 chill units[1] were released from dormancy, i.e. endodormancy, (Table 1: mean of all 4 models) between 16 November (700 U) and 1 March (1800 U). Fig. 2 shows that the results of the models are slightly different, because of the individual methods of chilling accumulation, but they converged with increasing C* (see also SD for the model mean in Table 1). For low chill crops (700 U) the mean difference of t_1 between the 4 models was 25.8 d and for high chill crops only 8.9 d. Model C3 showed the earliest date of dormancy release for all C* (Fig. 2). The reason is that the model has a relatively wide temperature range in which chilling is effective (≥1.5 to <12.5°C) and that temperatures ≥12.5°C do not reduce the accumulated chilling sum. The dates of t_1 for the Models C2 and C4 were similar. This could be due to warm spells in autumn and winter that reduce positive chill units in both models. The C* for the Wein-

[1]Chill unit (U): chilling hours according to the Weinberger-Eggert model (CH), chilling units according to the Utah and Positive Utah model (UCU and PCU), and chill portions calculated in the Dynamic model (CP/18)

Table 1. Average date of dormancy release (t_1, day of year), 1971–2000, for chilling models C1 to C4. C*: chilling requirement in chill units (U), SD′: spatial SD of 4253 grid points across Germany (see Fig. 3), *x*: mean of all models, SD: between models. Numbers >365 represent a value for the following year (superscript numbers: DOY of following year)

	C1		C2		C3		C4		Model mean	
C* (U)	t_1 (DOY)	SD′ (d)	t_1 (DOY)	SD′ (d)	t_1 (DOY)	SD′ (d)	t_1 (DOY)	SD′ (d)	*x* (DOY)	SD (d)
700	334.1	4.5	317.6	4.5	308.3	3.7	321.5	3.6	320.4	10.7
800	342.0	4.1	326.0	4.7	315.0	3.6	330.3	3.7	328.3	11.2
900	350.2	3.8	334.7	4.8	322.8	3.8	339.8	3.3	336.9	11.4
1000	359.0	3.7	344.4	6.0	332.1	3.9	349.1	3.2	346.2	11.2
1100	368.1^{03}	3.3	354.8	7.8	341.7	4.2	358.6	3.5	355.8	10.9
1200	376.7^{12}	3.4	366.1^{01}	10.0	352.0	6.0	368.7^{04}	4.0	365.9^{01}	10.3
1300	385.1^{20}	4.3	378.4^{13}	12.7	363.1	8.5	379.9^{15}	4.4	376.6^{12}	9.5
1400	394.0^{29}	5.3	390.0^{25}	14.5	375.6^{11}	11.6	390.3^{25}	5.2	387.5^{23}	8.2
1500	402.2^{37}	5.8	400.7^{36}	15.3	387.4^{22}	13.8	400.3^{35}	5.1	397.7^{33}	6.9
1600	409.9^{45}	6.3	410.3^{45}	15.7	399.2^{34}	14.7	409.5^{45}	5.5	407.2^{42}	5.4
1700	417.4^{52}	6.7	419.3^{54}	15.7	409.5^{45}	15.0	418.5^{54}	5.4	416.2^{51}	4.5
1800	424.7^{60}	6.8	427.7^{63}	15.6	418.8^{54}	15.1	426.8^{62}	5.5	424.5^{60}	4.0

berger-Eggert model was met at the latest date. Compared with the other models, the effective temperature range is smaller and the accumulation starts at lower temperatures (<7.2°C).

In the German lowlands, chill units accumulate mainly between early October and late February. In cold regions and at high altitudes accumulation may start in September and last until March. For low chill cultivars (700 to 1000 U), dormancy was released relatively uniformly across Germany before the end of the year (t_1 < 365 DOY). For cultivars with C* >1200 U, dormancy was released on average in the following year (t_1 > 365 DOY). C* was reached a few days later in the continental, SE regions than in the NW maritime regions (Fig. 3), because under current climate conditions the chilling process in the continental regions is usually interrupted by the winter, in which the hourly temperatures are predominantly <0°C (Müller-Westermeier et al. 1999). During this time no chill units are accumulated. This process continues after winter. In the NW parts of Germany, winter temperatures are generally higher, providing more chill units.

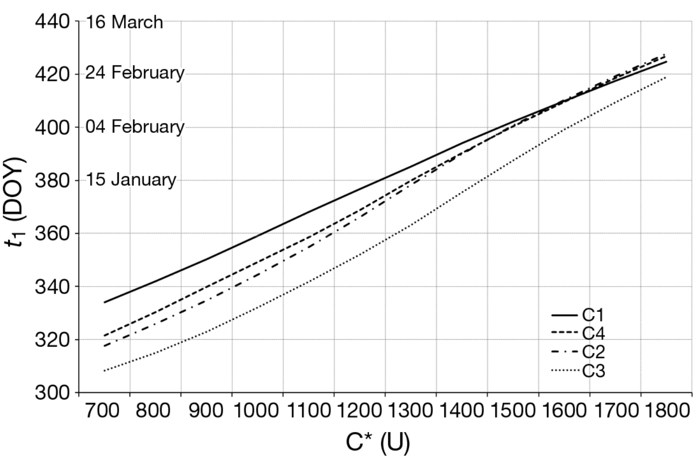

Fig. 2. Average date of dormancy release (t_1) in Germany (mean of 4253 GP), 1971–2000 (DWD data) for cultivars with a chilling requirement (C*) ranging from 700–1800 chill units (U: CH, UCU, PCU, CP/18). Numbers >365: value for the next year

3.2. Dormancy release for future climate conditions

To study the change in dormancy release due to rising temperatures, we repeated the calculations with the data from the regional climate model REMO-UBA. First we used the control run (C20) to calculate the release of dormancy for current climate conditions in the RCM (1971–2000). Then we computed the average date of t_1 for the REMO-UBA scenario period 2071–2100, to determine the differences in t_1 between scenarios A1B and C20 (Table 2).

For all C* values, Model C1 calculated a later date of dormancy release under future climate conditions (2071–2100, Fig. 4), as expected for a model approach with only 2 temperature thresholds when the temperatures in all months rise. Under warmer climate conditions, the beginning of chilling hour accumulation starts later, because the number of hours with temperatures within the optimal chilling range (0 to 7.2°C) in autumn would be lower than today. The strongest shift of t_1 with +40 d was found for a C* of 700 CH at the grid point 53.65°N, 7.45°E (NW Germany). Additionally, for Model C1 we found that the delay of t_1 decreased slightly with increasing C*, from 24.3 d for 700 CH to 11.6 d for 1800 CH on average (Table 2), probably because winter offers more hours with effective chilling temperatures; therefore, especially for high chill crops (1500 to 1800 CH), the later start of chilling hour accumulation was slightly compensated.

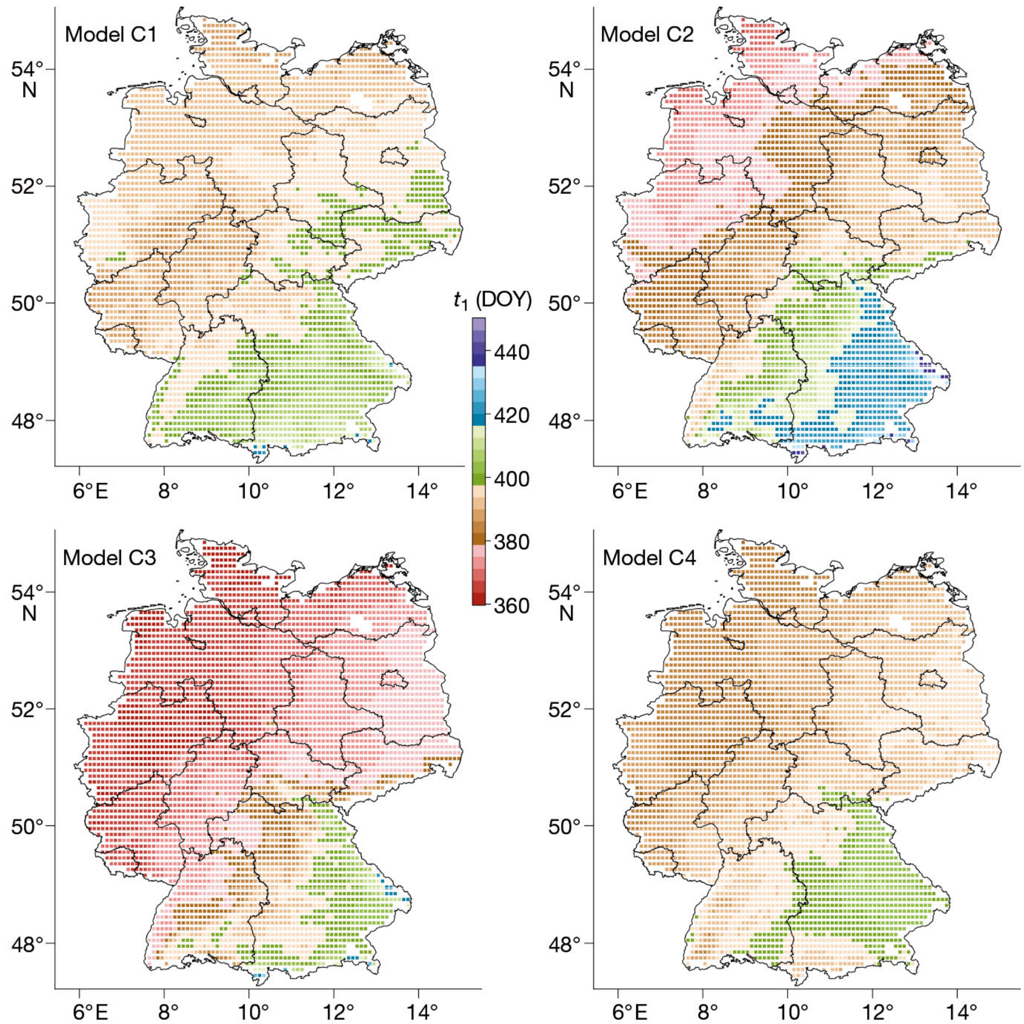

Fig. 3. Average date of dormancy release (t_1) for cultivars with a chilling requirement of 1400 chill units, based on DWD data for 1971–2000

Table 2. Average changes of dormancy release (Δt_1) between periods 2071–2100 (REMO-UBA, A1B) and 1971–2000 (REMO-UBA, C20) for chilling models C1 to C4. C*: chilling requirement in chill units (U), SD′: spatial SD of 4253 GP across Germany (see Fig. 4), x: mean of models C2 to C4, SD: between models

C* (U)	C1		C2		C3		C4		Mean (C2–C4)	
	Δt_1 (d)	SD′ (d)	Δt_1 (d)	SD′ (d)	Δt_1 (d)	SD′ (d)	Δt_1 (d)	SD′ (d)	x (d)	SD (d)
700	24.3	9.2	15.4	3.8	18.2	4.3	16.9	3.7	16.8	1.4
800	24.1	9.5	13.9	3.8	17.8	4.3	15.6	3.6	15.8	1.9
900	23.3	9.7	11.5	3.9	16.8	4.2	13.5	3.8	13.9	2.7
1000	23.0	9.8	6.8	4.1	14.1	4.2	10.5	3.8	10.5	3.7
1100	22.3	9.9	0.5	4.3	10.3	4.4	6.0	3.6	5.6	4.9
1200	21.0	10.1	−5.5	4.5	3.8	4.4	1.5	3.3	−0.1	4.8
1300	19.2	10.2	−11.0	4.5	−2.6	4.4	−3.0	3.4	−5.6	4.8
1400	17.4	10.3	−16.8	4.5	−9.0	4.3	−6.4	3.4	−10.7	5.4
1500	15.9	10.4	−21.3	4.8	−14.9	4.1	−8.5	3.3	−14.9	6.4
1600	14.4	10.4	−24.5	5.2	−20.1	4.1	−10.5	3.3	−18.3	7.2
1700	12.8	10.0	−26.6	5.7	−23.7	4.4	−11.6	3.6	−20.7	7.9
1800	11.6	9.4	−28.0	6.2	−26.3	4.8	−12.3	3.9	−22.2	8.6

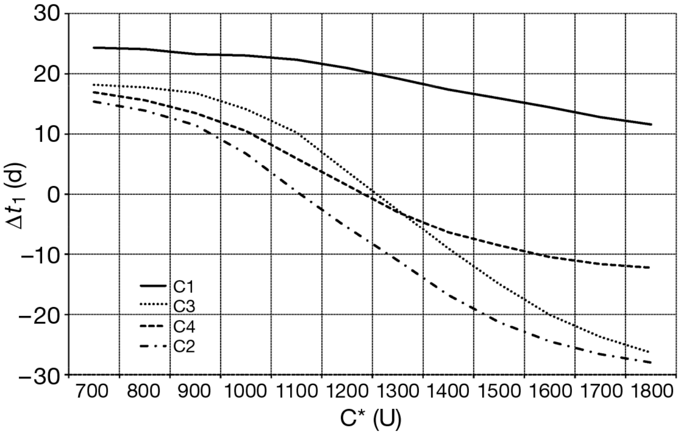

Fig. 4. Average changes in the date of dormancy release (Δt_1 in d) for the whole of Germany (mean of 4253 GP) for cultivars with a chilling requirement (C*) ranging from 700 to 1800 chill units (U: CH, UCU, PCU, CP/18), 2071–2100 (REMO-UBA, A1B) minus 1971-2000 (REMO-UBA, C20)

For the other 3 chilling models, the initial delay of t_1 up to ~1100 U (Model C2) or 1200 U (Models C3, C4) unexpectedly changed to an earlier dormancy release for high chilling cultivars, compared to the present (Fig. 4). For a C* ≥1200 U, dormancy release advanced in all models in the currently cold-winter, continental, SE regions of Germany. This is pronounced for 1400 chill units (Fig. 5). The strongest advancement of t_1 was −54 d in Model C2 for the Bavarian Forest (49° N, 13° E). Model C3 also showed a strong advancement in this region. In the mild-winter, maritime, NW regions, t_1 is slightly delayed (low/medium chill crops) or not changed at all for C* values up to 1800 U. For Models C2–C4, the strongest delay (21–23 d) was found for some grid points in the NW region. For Germany as a whole, the release of dormancy advanced with increasing values of C* because the areas with an earlier release of dor-

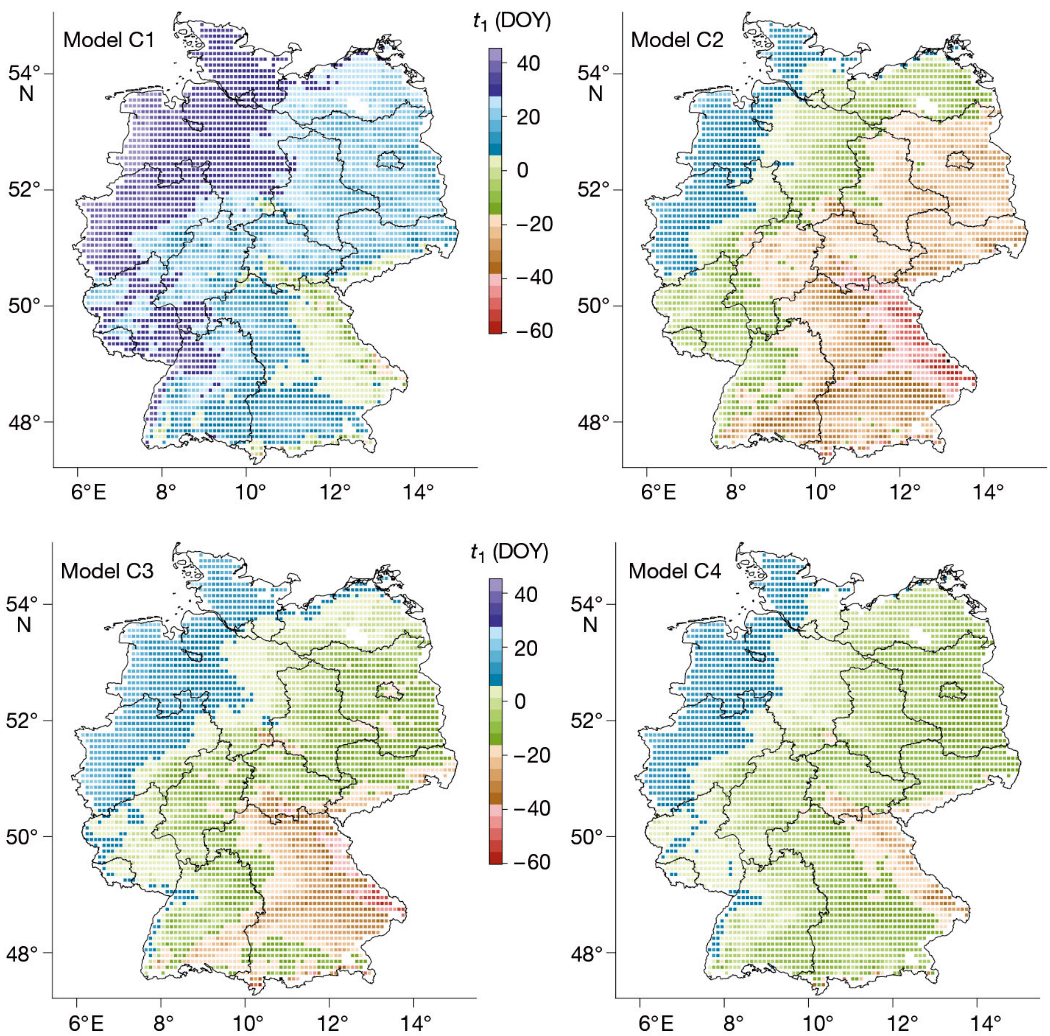

Fig. 5. Changes in the date of dormancy release (Δt_1) 2071–2100 (REMO-UBA, A1B) minus 1971-2000 (REMO-UBA, C20) across Germany for cultivars with a chilling requirement of 1400 chill units

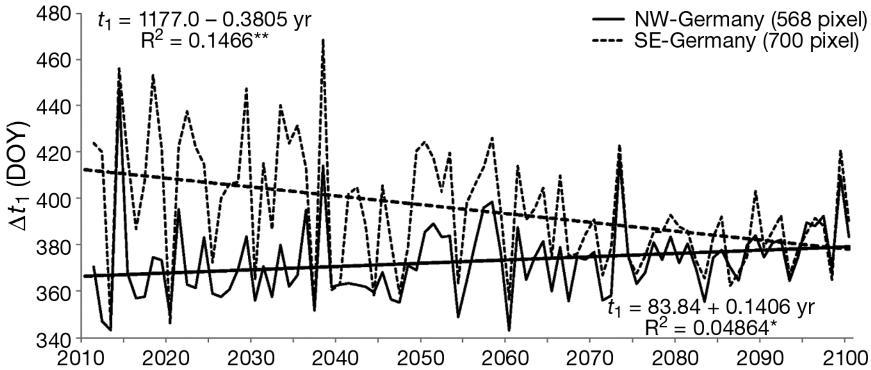

Fig. 6. Shifts in the date of dormancy release (t_1 in day of year [DOY]) in the north-western (>52° N, <10° E, 568 pixel) and south-eastern (<50° N, >10° E, 700 pixel) parts of Germany 2011–2100, for a cultivar with a chilling requirement of C* = 1400 UCU according to model C2. Significant trends: **$p < 0.01$, *$p < 0.05$

mancy extend from SE to NW due to rising autumn and winter temperatures. As result of these regional differences, by the end of the 21st century, C* = 1400 UCU may be fulfilled in mid-January in both regions (Fig. 6). Thus, the currently observed contrast in t_1 could disappear in the future.

According to Model C1, the end of dormancy will be delayed by 12 to 24 d in the future (2071–2100, scenario A1B), depending on C* of a cultivar (Fig. 7, see also Fig. 2). The other models predict a delay in t_1 for low chill varieties (700–1000 U), small changes for medium chill varieties (1100–1400 U), and an earlier end of winter dormancy for crops with a C* of 1500–1800 U.

4. DISCUSSION AND CONCLUSIONS

Chilling models are only proxies and a simplification of the complex biological processes that lead to a release of dormancy for perennial trees (Campoy et al. 2011). This study emphasizes that some differences between the results of the different chilling models exist. This was also stated by Campoy et al. (2012) and Luedeling & Brown (2011), who analysed model performance in different climate regions. Model C1 showed a relatively transparent behaviour. Rising temperatures lead to a delay of t_1 nearly everywhere in Germany up to a maximum of +40 d in NW Germany for 700 CH. The behaviour of the other 3 models was different but comparable among them. An initial delay in the release of dormancy across Germany turned into an earlier timing of t_1 with increasing C*. Among these models, the Dynamic model showed the smallest change. Some authors claim that the simple Weinberger-Eggert model is outdated (Darbyshire et al. 2011) or has strong limitations (Dennis 2003, Pérez et al. 2008). The significantly different results of Model C1 in response to climate change, compared to Models C2–C4, would support this hypothesis. The reason is probably that Model C1 is not able to consider the negation of accumulated chilling hours by high temperatures as observed in some chilling experiments (Richardson et al. 1974).

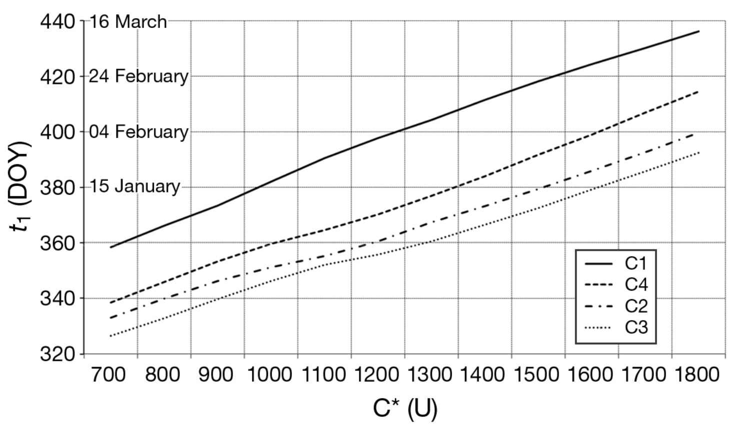

Fig. 7. Average future dates of dormancy release (t_1 in day of year [DOY]), 2071–2100 (mean of 4253 GP) for cultivars with a chilling requirement (C*) ranging from 700 to 1800 chill units (U: CH, UCU, PCU, CP/18) in Germany. Numbers >365: value for the next year

If we follow this assumption and if we only consider the results of Models C2–C4, we can state that even in the future, dormancy will probably be released soon enough for a wide range of fruit crops in Germany to ensure a timely start of reproductive development. This statement is supported by the fact that the areas in which t_1 is unchanged or advanced exceeds the regions where it is delayed. For crops with a medium C* of ~1100 to 1400 U, the release of dormancy did not delay more than 10 d (C3) on average, due to rising temperatures. The maximum delay at some individual grid points did not exceed 23 d in the NW region. More pronounced was the advanced release of t_1 with increasing C* up to −63 d for 1800 U in the SE regions (Models C2, C3; Model C4: −43 d), reflecting the regional contrast across Germany. In Fig. 6 we have seen that the delay in the maritime regions did not exceed the date of t_1 that is currently observed in the cold-winter regions. A later release of dormancy has much stronger implications for fruit growers (see Introduction) than an earlier dormancy completion. The latter one could lead to an earlier beginning of leafing or blossoming in spring if the environmental conditions (temperature, daylength) are favourable for the development of the buds and if the stage of ecodormancy is not significantly extended. The results of this analysis are also important for phenological modellers, as future changes in the timing of t_1 strongly depend on the region. For this reason, we recommend the use of combined chilling/forcing models to project possible shifts in the timing of spring phenological events due to climate change. In order to model the beginning of fruit tree blossom, Cesaraccio et al. (2004), Rea & Eccel (2006), Chmielewski et al. (2011), Blümel & Chmielewski (2011), and Matzneller et al. (2012) have used those models. The best results were always achieved using the combination of Model C4 with the GDD approach, which was modified by a daylength term (Blümel & Chmielewski 2012). On the basis of these combined models we optimized realistic values for C^*, which ranged between 800 CP/18 for peach and about 1300 CP/18 for apple, cherry, pear, and plume (Blümel & Chmielewski 2011). Luedeling & Brown (2011) also concluded that the CP from Model C4 is the most robust and transferable unit in different climate change scenarios.

Finally, it is important to validate the different chilling models on experiments that track the release of dormancy by molecular biological techniques, because we have found some differences among the model results (even among C2–C4). These methods could help to select those models which are most suitable to calculate t_1 for climate conditions in Germany. We think that this kind of research is necessary to achieve further noticeable progress in phenological modelling. First experimental and analytical studies in this direction have started at Humboldt University in cooperation with the University of Potsdam (Götz et al. unpubl.).

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