



Spring phenology in subtropical trees: Developing process-based models on an experimental basis

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ABSTRACT

Process-based phenological models are currently used for assessing the effects of climatic warming on the timing of spring phenological events, such as leafout and flowering, in trees. However, the biological realism of the models may be undermined by the practices of often formulating the models solely on the basis of observational records of the phenological event rather than addressing the physiological processes actually modelled. Here we introduce a framework for developing process-based phenological models on the basis of experiments explicitly designed for this purpose and apply the framework to developing process-based models for leafout in four subtropical tree species. Our method is based on a hypothetico-deductive approach, where the air temperature responses of the simulated processes are inferred from their implications for the occurrence and timing of leafout in the experimental conditions. That approach has only rarely been taken with boreal or temperate trees, and to the best of our knowledge, never before with subtropical trees. Big differences were found between the four species in the air temperature responses modelled, and these differences implied major differences in the dormancy dynamics predicted for the four species. Together with the results of a recent modelling study based on observational data, our results highlight the importance of experimental studies for the development of biologically realistic process-based models of spring phenology in trees. The framework developed in the present study can be applied to developing such models for all tree species that show the phenomena of rest (endodormancy) and chilling requirement, no matter whether the trees are boreal, temperate, or subtropical.

1. Introduction

In many terrestrial biomes of the world, shifts in the spring phenology of plants are amongst the most important effects of the ongoing climate change (Polgar and Primack, 2011). As a rule, warming has accelerated the spring phenology over the last decades (Menzel et al., 2006; Piao et al., 2019), but more recently a levelling off of the acceleration has also been found (Fu et al., 2015). Changes in the spring phenology affect essential ecosystem processes, such as the cycling of water, carbon and nutrients (Kramer and Hänninen, 2009; Richardson et al., 2009), ecosystem productivity (Keenan et al., 2014), plant-animal

relationships (Senior et al., 2020), population dynamics and competition of plant and animal species (Delpierre et al., 2017; Zettlemoyer et al., 2019), and ultimately, shifts in the geographical ranges of species (Chuine and Beaubien, 2001; Chuine, 2010).

The effects of future climatic warming on boreal and temperate trees are currently often assessed by means of process-based models of tree spring phenology (Vitasse et al., 2011; Chuine et al., 2016; Ford et al., 2016; Wang et al., 2020). These models address the effects of air temperature on two processes regulating the timing of spring bud burst; in the modelling context, ‘bud burst’ is used in this study as a generic concept, including all particular cases of the visible spring phenological

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events of trees, such as leafout of vegetative buds, or anthesis in the flower buds: 1) rest break (endodormancy release), and 2) the microscopic ontogenetic development (cell growth, division, and differentiation) within the bud, which leads to the visible bud burst (Chuine, 2000; Chuine et al., 2013; Hänninen, 2016).

After growth cessation in autumn, the buds of boreal and temperate trees attain the state of rest (endodormancy; Lang et al., 1987), where bud burst and growth onset are prevented by physiological factors inside the buds (Fuchigami et al., 1982; Hänninen and Tanino, 2011). The growth-arresting conditions are removed by prolonged exposure (days to months) to low chilling temperatures (Cooke et al., 2012; Tylewicz et al., 2018), traditionally, temperatures near +5 °C have been regarded as necessary for chilling (Sarvas, 1974). This is the chilling requirement of rest completion (Hänninen, 1995, 2016), which prevents a premature growth onset during mild periods in autumn and winter, which would lead to frost damage during subsequent periods of frost (Cannell, 1985; Hänninen, 1991; Zohner et al., 2020), a phenomenon more recently called ‘false springs’ (Marino et al., 2011; Chamberlain et al., 2019). After the chilling requirement is met, the phase of quiescence (ecodormancy, Lang et al., 1987) is attained (Fuchigami et al., 1982; Hänninen and Tanino, 2011). During quiescence, bud burst and growth onset are prevented by low air temperatures only, so that ontogenetic development occurs in relatively high forcing temperatures (Sarvas, 1972, 1974). Ontogenetic development may take place during the rest period already, but only at a reduced rate in comparison with its rate under similar ambient conditions during quiescence (Hänninen, 2016). Visible bud burst occurs as a result of prolonged exposure (days to months) to forcing temperatures (the high-temperature requirement of growth onset, Hänninen, 1995, 2016).

In the last few decades there have been great advances in insights into the molecular control of rest break (Falavigna et al., 2015; Tylewicz et al., 2018; Miotto et al., 2019), and preliminary steps have been taken towards bringing these insights into mathematical models for flowering phenology (Bhalerao et al., 2018). However, it is currently unclear how the molecular mechanisms found for flowering phenology translate into directly quantitative indicators of the rest status of foliar buds. Ontogenetic development can be observed by means of microscopic observations, but due to the destructive sampling and the large amount of labour required, such measurements have only rarely been used in the process-based modelling (Sarvas, 1972, 1974; Viherä-Aarnio et al., 2014). Given that background, we take the position that process-based models for bud burst are best developed on the basis of the occurrence and timing of bud burst in experiments that are explicitly designed for determining the air temperature responses included in the models (Hänninen et al., 2019). When doing so, we apply the hypothetico-deductive (HDM) scientific method, where models for processes not observed are developed and tested on the basis of their predictions for phenomena that are observable in the experimental conditions.

In boreal and temperate trees, the chilling requirement of rest break has been studied for a hundred years: the phenomenon was first reported by Coville (1920). Given this background, it is surprising that the rest period and the chilling requirement in subtropical trees have not been experimentally examined until recently, when Du et al. (2019), Song et al. (2020) and Zhang et al. (2021a, b) showed that subtropical trees also exhibit the rest period and require chilling for rest completion. Further, Zhang et al. (2021a) have recently shown that the air temperature responses of the dormancy processes in subtropical trees are different from those in the more northern ones. This points to the importance of developing specific process-based tree phenology models for subtropical trees (Jewaria et al., 2021). To our knowledge, no

process-based model addressing rest break and ontogenetic development towards spring bud burst has been developed for any subtropical tree species by using the ecophysiological approach, where the HDM method and explicitly designed experiments are used for model development. Here, we 1) first introduce a methodological framework for the ecophysiological approach, and 2) by using the experimental results of Zhang et al. (2021a) and additional experimental data gathered for the present study, we apply the framework to developing process-based tree phenology models for four subtropical tree species. We hypothesize that the process-based models developed on the basis of explicitly designed experiments will reveal differences in the dormancy phenomena between the four subtropical tree species examined.

2. Materials and methods

2.1. The overall structure and terminology of the model

The process-based models were constructed by using a modular model structure consisting of three sub-models (Fig. 1; Hänninen, 1990, 2016; Hänninen and Kramer, 2007; Lundell et al., 2020).

In the models, air temperature, $T(t)$, affects the timing of bud burst via two different causal chains. First, the effects of chilling temperatures on rest break (endodormancy release) in the buds are addressed in Sub-model I (Fig. 1). Chilling temperatures regulate the rate of rest break, $R_r(t)$, which determines the state of rest break, $S_r(t)$, via integration. Rest completion is predicted to occur when $S_r(t) = 100\%$. After that the value of $S_r(t) = 100\%$ is retained until the end of the simulation at the predicted time of bud burst. $S_r(t)$ determines the value of the ontogenetic competence, C_o (Sub-model III), which is a [0,1]-multiplier for translating the restrictions caused by the rest status of the buds into the ontogenetic development. Second, the effects of high temperatures on the microscopic ontogenetic development inside the buds leading to visible bud burst (cell growth, division, and differentiation) are addressed in Sub-model III (Fig. 1). High temperatures determine the potential rate of ontogenetic development, $R_{o,pot}$, i.e., the rate unrestricted by the rest condition (Sub-model II). Finally, the realized rate of ontogenetic development, R_o , is obtained as $R_{o,pot}$ multiplied by C_o (Figs. 1 and S1). With $C_o = 0$, there is no ontogenetic development regardless of the prevailing temperature. At the time of rest completion ($S_r = 100\%$), the value of $C_o = 1$ is attained, and the rate of ontogenetic development, R_o , is no longer restricted by the rest status of the bud. R_o determines the state of ontogenetic development, S_o , via integration, and when S_o attains the value of 100%, bud burst is predicted to occur (Fig. 1). A new annual cycle is initiated on the next day of rest initiation, t_0 , by setting $S_r = 0\%$ and $S_o = 0\%$. In the present study, the model was applied with a time step of one hour, with the hourly air temperature used as input in the simulations.

2.2. Experimental data

The experiments were carried out on the Zhejiang A&F University campus (30°14'N, 119°42'E) in Hangzhou, southeastern China. Hangzhou has a subtropical, monsoonal climate (Peel et al., 2007; Fig. S2). The mean annual air temperature is +15.6 °C, and the mean monthly air temperature ranges from +4.5 °C in January to +28.9 °C in July. In winter, episodic slight frosts ($T > -10$ °C) occur frequently. The frost-free season lasts from mid- to late March till mid- to late November (Zhang, 2015).

Process-based tree phenology models were constructed for four subtropical tree species common in subtropical southeastern China: *Castanopsis sclerophylla* (Lindl.) Schott, *Phoebe chekiangensis* C.B. Shang

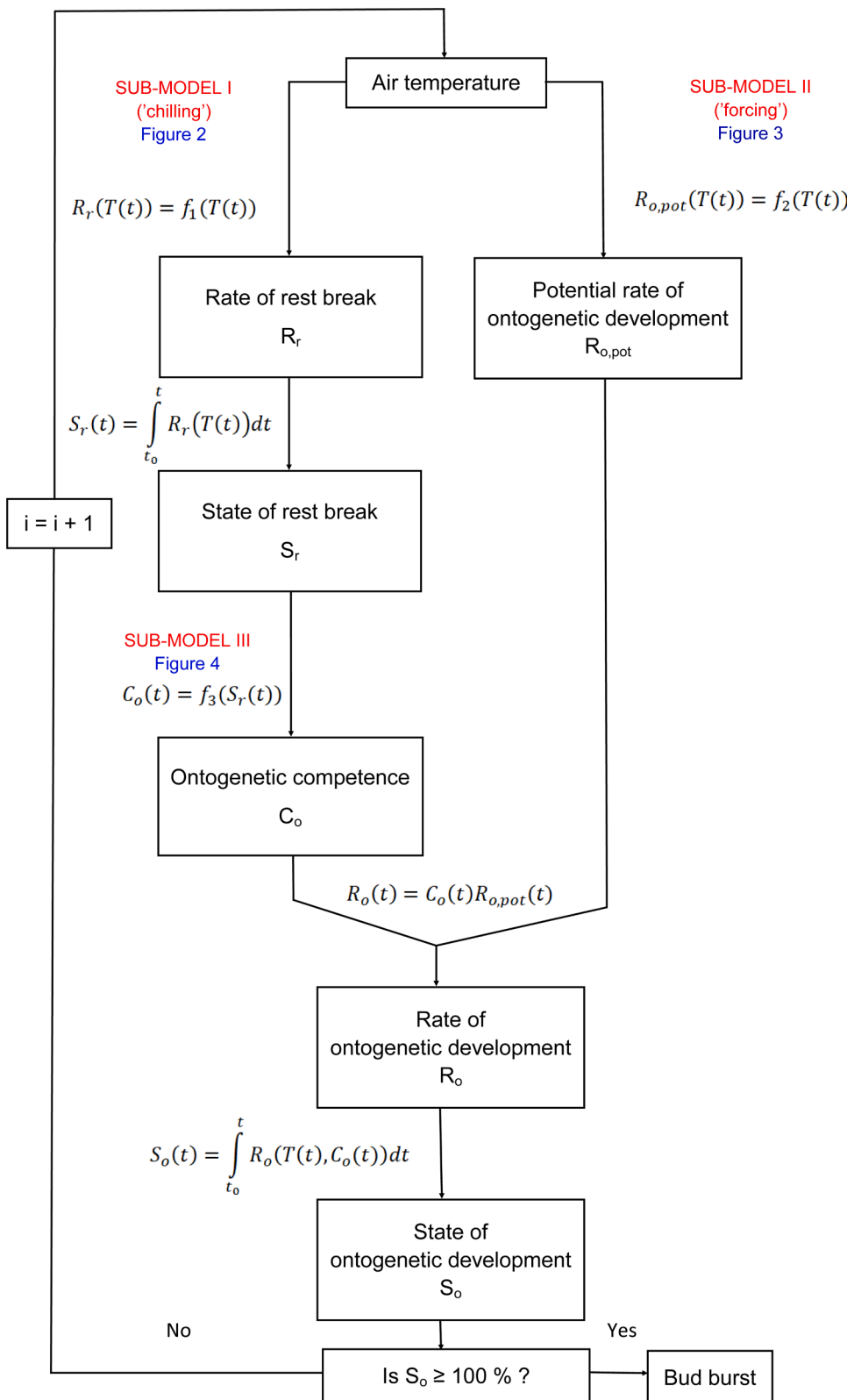


Fig. 1. The flow diagram of the modular overall model adopted in the present study for process-based modelling of spring phenology in trees (Hänninen, 1990, 2016; Hänninen and Kramer, 2007; Lundell et al., 2020). The overall model consists of three sub-models, each one addressing the corresponding particular air temperature response that affects the timing of bud burst ('bud burst' is used as a generic concept here, including all particular cases of the spring phenological events, such as leafout of vegetative buds or anthesis in the flower buds). The black and red fonts indicate the general structure of the overall model. The references to figures in the blue font indicate the introduction of the experimental information to the three sub-models carried out in the present study, by giving particular operational forms for the three respective general response functions f_1 , f_2 , and f_3 . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

ex P.T. Li, *Pseudolarix amabilis* (Nelson) Rehd., and *Torreya grandis* Fort. ex Lindl (Editorial Committee for Flora of the Chinese Academy of Sciences, 1990; Fig. S2). *Castanopsis* and *Phoebe* are broadleaved while *Pseudolarix* and *Torreya* are coniferous. For all species, first-year container seedlings were used in the experiments. To develop the models, both previously published (Autumn experiments, Zhang et al., 2021a) and original (Spring experiments) data were used.

In the autumn experiments carried out in 2017 – 2019 by Zhang et al. (2021a), data for Sub-models I and III were gathered by addressing the effects of chilling on rest break, and subsequently, on the ontogenetic competence of the buds (Fig. 1). The experimental seedlings were first subjected to chilling for periods of varying duration, then transferred to growth-promoting forcing conditions with a constant air temperature of +20 °C (Zhang et al., 2021a). The chilling treatments were carried out in

growth chambers at four constant temperatures: +5 °C, +6 °C (for *Torreya* seedlings only), +10 °C, and +15 °C. In the forcing conditions, a regrowth test was carried out by observing the occurrence and timing of leafout. In the present study, the seedling leafout is referred to with the generic concept 'bud burst' in the modelling context and in connection with the standard variables BB% (bud burst percentage) and DBB (days to bud burst in the forcing conditions) (Fig. 1). Accordingly, for each observed seedling showing leafout, the value of DBB was calculated, and for each treatment representing a given duration of chilling at a given chilling temperature, the value of BB% was calculated.

In the three spring experiments carried out for the present study in the years 2018 – 2020, data for Sub-model II were gathered by addressing the effects of the air temperature on the potential rate of ontogenetic development. Until the start of the experiment, the experimental seedlings overwintered in natural conditions on the Zhejiang A&F University campus (30°14N, 119°42E) in Hangzhou, southeastern China. In order to make sure that the actual rate of ontogenetic development observed in the experiment represented the potential rate, the spring experiments of all the three years 2018 – 2020 were started on 13 February, after the chilling requirement in natural conditions had been met in all four species (Zhang et al., 2021a). In each year, we transferred ten replicated seedlings of each species from natural outdoor conditions to forcing growth chambers (E-Lotus Technology Co., Beijing, China) with several constant air temperatures ranging from 10 to 28 °C (Table 1). The seedlings were prepared for the experiments in the same way as in the autumn experiments (Zhang et al., 2021a). In all the forcing chambers, day length was 12 h, PPFD 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, relative humidity 70–80%, and concentration of CO₂ 300–400 ppm. Temperature of the chambers was monitored with iButton (Model DS1912L, Embedded Data Systems Co., Ltd, KY, USA). Leafout was observed visually, as had been done in the autumn experiments (Zhang et al., 2021a). For each experimental seedling, the days to bud burst in the forcing conditions, DBB, was calculated.

2.3. Framework for formulating the models on the basis of experimental data

2.3.1. Sub-model I

The rate of rest break $R_r(T')$ at any constant temperature T' was determined experimentally as the reciprocal of the time required for rest completion, Δt , at that temperature (Sarvas, 1974), multiplied by 100 (Eq. (1) in Table 2). Because of the multiplier 100, the unit of R_r is % h^{-1} , so that the value of $R_r(T')$ indicates how many per cent of the cumulative physiological processes required for rest completion take place within one hour.

The value of the Δt was determined on the basis of the results of the autumn experiments (for experiment description, see above). First, the values of bud burst percentage, BB%, and days to bud burst, DBB, were plotted against the duration of chilling. By means of the scatter plots thus obtained, the value of Δt was determined by two rules: First, it was

required that $\text{BB}\% \geq 80\%$ for the chilling duration corresponding to Δt . Second, it was required that the value of DBB decreased to a threshold value, DBB_{RC} , determined by the levelling off of the DBB curve in the +5 °C chilling experiment. To that end, an exponential function f_4 was first fitted to the scatter plot of the +5 °C chilling experiment, representing the DBB value of each seedling as a function of the duration of chilling (Fig. S3a and Eq. (2) in Table 2). The value of Δt was then determined for the +5 °C chilling treatment as equal to the duration of chilling x where the value of the first derivative of the exponential function is equal to -0.3 (Fig. S3a and Eqs. (3)–(5) in Table 2).

Next, the exponential function f_4 (Eq. (2) in Table 2) was fitted to the scatter plots of +6 °C, +10 °C (Fig. S3b) and +15 °C chilling treatments. For them, the value of Δt was determined as the duration of chilling implying the same value of $\text{DBB} = \text{DBB}_{\text{RF}}$ as was obtained with the +5 °C chilling treatment (Fig. S3 and Eq. (6) in Table 2).

The Δt values obtained (Table 3 and Fig. S4) were plugged into the equation determining the rate of rest break (Eq. (1) in Table 2), thus getting four (for *Torreya*) or three (for the other three species) empirical data points for R_r in the temperature range of +5 to +15 °C (see Fig. 2 in the Results Section). In that temperature range, the temperature response of the rate of rest break (function f_1 of Sub-model I in the overall model, Fig. 1) was determined by fitting a direct line to the scatter plot representing the observed R_r as a function of temperature. Following Sarvas's (1974) observations with a boreal *Betula* species, a lower threshold for the rest-breaking temperature range was a priori assumed at -3.4 °C. It was assumed, then, that below +5 °C, R_r would drop from its maximum value (obtained at +5 °C) to zero at -3.4 °C. Similarly, an upper threshold for the rest-breaking temperature range was a priori assumed at +20 °C, so that R_r was assumed to drop from its value at +15 °C to zero at +20 °C. In all, two piece-wise linear temperature responses were obtained for the general form of Sub-model I, one for *Pseudolarix* and *Torreya* and one for *Castanopsis* and *Phoebe* (Eqs. (7) and (8) in Table 2, respectively).

2.3.2. Sub-model II

For Sub-model II, the potential rate of ontogenetic development at any constant temperature T' , $R_{o,\text{pot}}(T')$, was determined experimentally as the reciprocal of the days to bud burst, DBB, measured at the constant temperature T' after rest completion (Sarvas, 1972; Campbell, 1978), multiplied by 100 (Eq. (9) in Table 2). Because of the multiplier 100, the unit of $R_{o,\text{pot}}$ is % h^{-1} , so that the value of $R_{o,\text{pot}}(T')$ indicates how many per cent of the ontogenetic changes required for bud burst take place after rest completion within one hour. The values of $R_{o,\text{pot}}(T')$ were plotted against the experimental temperature T' . The air temperature response of $R_{o,\text{pot}}$ (function f_2 of Sub-model II in the overall model, Fig. 1) was formulated by fitting a sigmoidal function to the scatter plot (Eq. (10) in Table 2 and see Fig. 3 in the Results Section).

2.3.3. Sub-model III

By the definition of ontogenetic competence, C_o , the empirical value of C_o for a given seedling is zero if it shows no leafout during prolonged forcing, and by the same token, it is unity if its DBB is equal to the DBB representing seedlings which have just attained rest completion, i.e., equal to $\text{DBB}(\Delta t) = \text{DBB}_{\text{RC}}$ (Fig. S3). Between these two extremes, the value of C_o increases proportionally to the ratio of $\text{DBB}(\Delta t) / \text{DBB}$ of the seedling. In the calculation of the empirical values of C_o , two averaging methods were applied. First, the original DBB observations of the individual seedlings were replaced by the fitted exponential functions, f_4 (Eq. (2) in Table 2 and Fig. S4). Accordingly, the value of C_o for any duration of chilling x at a given constant chilling temperature was calculated as the ratio $f_4(\Delta t) / f_4(x)$. Second, in order to account for the seedlings showing little or no leafout, the value of C_o was set at zero for chilling treatments in which fewer than a half of the buds showed leafout (Eq. (11) in Table 2).

In Sub-model III, the value of C_o is calculated as a function of the state of rest break, S_r (function f_3 in the overall model, Fig. 1).

Table 1

Experimental temperatures applied in the spring experiments of 2018 – 2020 for formulating Sub-model II for seedlings of each of the four tree species examined.

Year	Experimental temperature
2018	+10 °C
	+17 °C
	+24 °C
2019	+12 °C
	+20 °C
	+28 °C
2020	+10 °C
	+15 °C
	+20 °C
	+25 °C

Table 2
Equations used in the study.

Explanation	Equation	Symbols
Sub-model I: Air temperature response of the rate of rest break		
Experimental determination of the rate of rest break.	$R_r(T') = 100 \frac{1}{\Delta t(T')} \quad (1)$	R_r = value of rest break in the experimental temperature T' (empirical data point for Sub-model I) Δt = duration of chilling (hours) needed for rest completion
Equation fitted to the DBB data for determining Δt in Eq. (1) for all chilling treatments.	$DBB(x) = f_4(x) = y_0 + a_1 e^{-b_1 x} \quad (2)$	DBB = modelled days to bud burst x = duration of chilling (days) y_0, a_1, b_1 = parameters (Fig. S3)
Equation used for determining Δt in Eq. (1) for the +5 °C chilling treatment. The first derivative of Eq. (2).	$\frac{dDBB}{dx} = -a_1 b_1 e^{-b_1 x} \quad (3)$	DBB = modelled days to bud burst x = duration of chilling (days) a_1, b_1 = parameters (Fig. S3)
Equation used for determining Δt in Eq. (1) for the +5 °C chilling treatment. Setting the threshold value for Eq. (3).	$\frac{dDBB}{dx} = -a_1 b_1 e^{-b_1 x} = -0.3 \quad (4)$	As in Eq. (3)
Equation used for determining Δt in Eq. (1) for the +5 °C chilling treatment. Implied by Eq. (4).	$\Delta t = x = -\frac{1}{b_1} \ln \frac{0.3}{a_1 b_1} \quad (5)$	As in Eq. (3)
Equation used for determining Δt in Eq. (1) for the +6, +10 and +15 °C chilling treatments. Implied by Eq. (2) when setting $DBB = DBB_{RC}$.	$\Delta t = x = -\frac{1}{b_1} \ln \frac{DBB_{RC} - y_0}{a_1} \quad (6)$	DBB_{RC} = days to bud burst corresponding to Δt in the +5 °C chilling treatment (Fig. S2b) Other symbols as in Eq. (3) The parameter values are reported in Fig. S3.
Sub-model I: general form of the equation for Pseudolarix and Torreya		
	$R_r(t) = \begin{cases} 0 & , T < -3.4^\circ C \\ k_1 \times T + d_1 & , -3.4^\circ C \leq T < +5^\circ C \\ k_2 \times T + d_2 & , +5^\circ C \leq T < +15^\circ C \\ k_3 \times T + d_3 & , +15^\circ C \leq T < +20^\circ C \\ 0 & , +20^\circ C \leq T \end{cases} \quad (7)$	R_r = rate of rest break T = air temperature $k_1, k_2, k_3, d_1, d_2, d_3$ = parameters (see Table 5 in the Results section)
Sub-model I: general form of the equation for Castanopsis and Phoebe		
	$R_r(t) = \begin{cases} 0 & , T < -3.4^\circ C \\ k_1 \times T + d_1 & , -3.4^\circ C \leq T < +5^\circ C \\ d_2 & , +5^\circ C \leq T < +15^\circ C \\ k_3 \times T + d_3 & , +15^\circ C \leq T < +20^\circ C \\ 0 & , +20^\circ C \leq T \end{cases} \quad (8)$	R_r = rate of rest break T = air temperature k_1, k_3, d_1, d_2, d_3 = parameters (see Table 5 in the Results section)
Sub-model II: air temperature response of the potential rate of ontogenetic development		
Experimental determination of the potential rate of ontogenetic development.	$R_{o.pot}(T') = 100 \frac{1}{DBB(T')} \quad (9)$	$R_{o.pot}(T')$ = potential rate of ontogenetic development in the experimental temperature T' (empirical data point for Sub-model II) DBB = measured days to bud burst (expressed in hours)
Sub-model II: general form of the equation	$R_{o.pot}(T) = \frac{a_2}{1 + e^{b_2(T - c_2)}} \quad (10)$	$R_{o.pot}$ = modelled potential rate of ontogenetic development T = air temperature a_2, b_2, c_2 = parameters (see Table 6 in the Results section)
Sub-model III: dependence of ontogenetic competence, C_o , on the state of rest break, S_r		
Experimental determination of ontogenetic competence.	$C_o(x) = \begin{cases} 0 & , BB\%(x) < 50\% \\ f_4(\Delta t) & , BB\%(x) \geq 50\% \end{cases} \quad (11)$	C_o = ontogenetic competence (empirical value) x = duration of chilling in days BB% = bud burst percentage f_4 = exponential function fitted to the DBB data (= Eq. (2) above) Δt = duration of chilling required for rest completion, as determined experimentally by Eqs. (2)–(6)
Sub-model III: general form of the equation	$C_o(S_r) = \begin{cases} 0 & , S_r < S_{r.min} \\ a_3 S_r + 1 - 100a_3 & , S_r \geq S_{r.min} \end{cases} \quad (12)$	C_o = modelled ontogenetic competence S_r = state of rest break $S_{r.min}, a_3$ = parameters (see Table 7 in Results section)
Generation of hourly temperature data for simulations (Zohner et al., 2020)		
Converting daily minimum and maximum temperatures into hourly temperatures.	$T_{hour} = \frac{(T_{max} - T_{min})}{2} \times \sin\left(\frac{\pi}{12} \times time_{day} - \frac{\pi}{2}\right) + \frac{(T_{max} + T_{min})}{2} \quad (13)$	T_{hour} = hourly temperature T_{max} = daily maximum temperature T_{min} = daily minimum temperature $time_{day}$ = hour within the day

Accordingly, the empirical values of C_o (Eq. (11) in Table 2) were plotted against S_r . $S_r(x)$ was calculated for each duration of chilling x at a given constant chilling temperature as $100 x/\Delta t$. This simple formula is implied in the assumption that at any constant air temperature, rest break progresses at a constant rate. In order to account for empirical zero

values of C_o with small values of S_r , a piece-wise linear form was assumed for function f_3 , such that $C_o = 0$ below a threshold value of $S_r = S_{r,min}$ and increases to $C_o = 1$ at $S_r = 100\%$ above the threshold (Eq. (12) in Table 2).

Table 3

Duration of chilling, Δt , required at the experimental chilling temperatures for rest completion in seedlings of each of the four tree species examined. The values of Δt are indicated both in hours, as used in the model development (Eq. (1) in Table 2), and in days, as used in the plots to determine the values (Figs. S2 and S3).

Tree species	Chilling temperature	Δt , days	Δt , hours
<i>Castanopsis sclerophylla</i>	+5 °C	68.70	1649
	+10 °C	68.95	1655
	+15 °C	56.25	1350
<i>Phoebe chekiangensis</i>	+5 °C	33.72	809
	+10 °C	33.85	812
	+15 °C	19.34	464
<i>Pseudolarix amabilis</i>	+5 °C	52.70	1265
	+10 °C	69.45	1667
	+15 °C	102.81	2467
<i>Torreya grandis</i>	+5 °C	26.31	631
	+6 °C	56.33	1352
	+10 °C	37.56	901
	+15 °C	69.51	1668

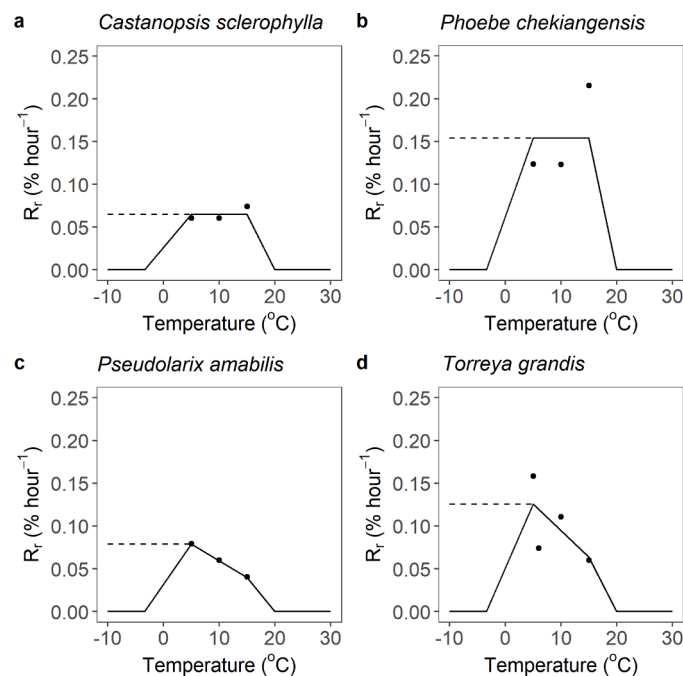


Fig. 2. Sub-model I for each of the four tree species examined, representing the temperature response of the rate of rest break, R_r , (function f_1 in the overall model, Fig. 1). The data points were determined on the basis of the experimental results of Zhang et al. (2021a). The equations for f_1 are presented in Table 2 (Eqs. (7) and (8)) and the parameter values in Table 5. The value of the model variable R_r indicates how many per cent of the physiological changes required for rest completion take place in one hour. The value $R_r = 0.1\% \text{ hour}^{-1}$, for instance, indicates that 1000 h are required at the particular temperature for rest completion. The dotted lines refer to the modified model used in the sensitivity analysis that addressed the uncertainty caused by the lack of data for temperatures under +5 °C.

2.4. Tests of the models with independent leafout data and the dormancy dynamics predicted by the models

For testing the models developed, three sets of independent leafout observations were used. Starting on 23 November for each annual cycle, the model for each species was run on an hourly basis until it predicted leafout to occur. The predicted leafout dates were then compared with

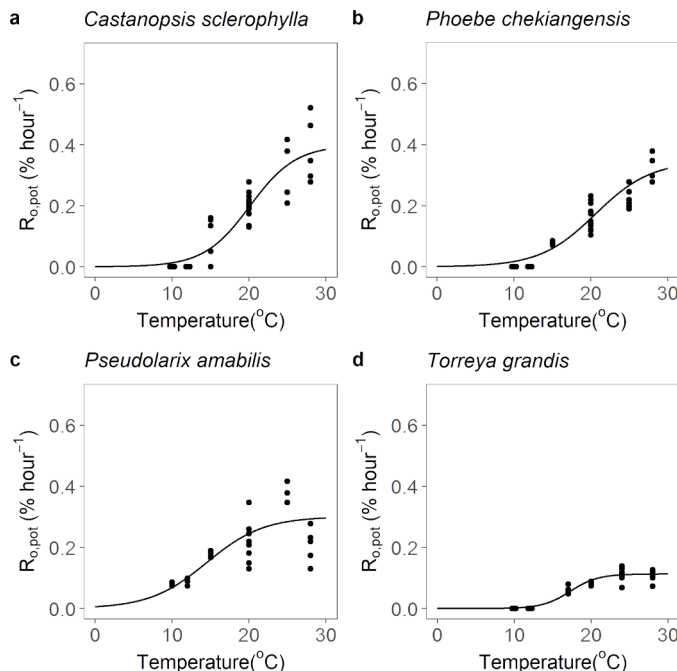


Fig. 3. Sub-model II for each of the four tree species examined, representing the temperature response of the potential rate of ontogenetic development, $R_{0,pot}$, (function f_2 in the overall model, Fig. 1). Function f_2 is formulated according to Eq. (10) (Table 2) with the parameter values presented in Table 6. The potential rate of ontogenetic development indicates the rate at rest completion, i. e., when the chilling requirement has been met and the rate is no longer restricted by the rest condition of the bud. More specifically, $R_{0,pot}$ indicates how many per cent of the ontogenetic changes within the bud required for leafout take place after rest completion in one hour. The value $R_{0,pot} = 0.2\% \text{ hour}^{-1}$, for instance, indicates that at the particular temperature, 500 h after rest completion are required for leafout.

the observed ones.

The first test of the models was carried out with seedlings kept on our campus in natural conditions from autumn 2018 to spring 2019. The predicted leafout was thus tested in one year only, and rather than testing the model, the main purpose here was to illustrate the dynamics of rest break and ontogenetic development predicted by the models. To that end, we calculated the predicted state of rest break, S_r , ontogenetic competence, C_o , and the state of ontogenetic development, S_o , for the period of autumn 2018 to spring 2019 in natural conditions on the Zhejiang A&F University campus (Zhang et al., 2021a). The calculations were based on hourly air temperature records collected with iButtons (Model DS1912L, Embedded Data Systems Co., Ltd, KY, USA) in natural conditions. In order to illustrate the dormancy dynamics predicted by the models, the values of S_r , C_o , and S_o were plotted over time from the start of the simulation till the predicted day of leafout. Leafout predicted by the models was compared with leafout observations made in natural conditions on the campus in spring 2019. To that end, 10 seedlings were monitored for leafout in the natural conditions. The seedlings had been raised like those used in the experiments carried out for model development. Bud development was observed and the timing of leafout was determined in the same way as in the experiments producing the experimental data for model development (Zhang et al., 2021a).

Second, the models were tested against independent observational records of leafout in mature trees, obtained from the Chinese National Ecology Science Data Centre (Table 4). No phenological records were available for testing the model developed for leafout in *Torreya*. The daily minimum (T_{min}) and maximum (T_{max}) temperatures were obtained from meteorological stations of the China National Meteorological Information centre located near the phenological stations (Table 4). The hourly temperature data needed in the simulations was not available in

Table 4

The stations where phenological records were collected and the corresponding meteorological stations that provided air temperature data; both data sets were used in the present study for independent testing of process-based tree phenology models. The phenological data comprised the leafout of vegetative buds in mature trees (Chinese National Ecology Science Data Centre, www.cnern.org.cn; China Meteorological Administration, 1993). All temperature data were provided by the China National Meteorological Information centre (www.data.cma.cn).

Station index	Phenological station			Meteorological station			Years	Tree species
1	Changsha	28°06' N	113°00' E	Changsha	28°07' N	113°00' E	2005–2008	<i>Castanopsis sclerophylla</i> <i>Phoebe chekiangensis</i> <i>Pseudolarix amabilis</i>
2	Yinxian	29°36' N	121°12' E	Yinxian	29°31' N	121°20' E	1984–1996	<i>Pseudolarix amabilis</i>
3	Guilin	25°13' N	110°15' E	Guilin	25°09' N	110°06' E	2005, 2006, 2008	<i>Pseudolarix amabilis</i>

the temperature records, which is why the hourly temperatures were generated from the daily temperature data following Zohner et al. (2020) (Eq. (13) in Table 2).

Third, the models were tested with independent leafout data collected in a whole-tree chamber (WTC) warming experiment on the Zhejiang A&F University campus in autumn, winter and spring 2019–2020. In the experiment we applied a complete 3×3 random design with nine treatments combining three levels of both spring and winter warming: ambient temperature, ambient plus two degrees warming, and ambient plus four degrees warming. The winter warming treatments were conducted from 10 November 2019 to 10 February 2020 and the spring ones from 11 February 2020 until the observed leafout. In each treatment we had eight replicated first-year seedlings of each of the four species. The seedlings had been raised like those used in the experiments carried out for model development (Zhang et al., 2021a). Three WTCs (E-Lotus Technology Co., Beijing, China) were used in the experiment, one for each temperature level applied.

The nine temperature treatments were realized by moving seedlings from chamber to chamber. At the beginning of the experiment on 10 November 2019, 24 seedlings of each species were put in each of the three WTCs representing the corresponding three temperature levels. On 11 February 2020, three sub-groups of eight seedlings were randomly sampled in each chamber. One sub-group remained in the same chamber and the other two were transferred, each into one of the WTCs representing the other two temperature levels. In this way, nine temperature treatments simulating the current climate and eight different cases of climatic warming were created. The hourly air temperature records in each chamber were collected with iButtons (Model DS1912L, Embedded Data Systems Co., Ltd, KY, USA). In the calculations, the mean value of the recorded hourly temperatures was used. Leafout was determined in the same way as in the experiments producing the experimental data for model development (Zhang et al., 2021a).

2.5. Sensitivity analysis

In order to examine the potential role of temperatures below $+5^\circ\text{C}$ in the rest break and the subsequent timing of bud burst, simulations of bud burst timing, with long-term air temperature data as input, were carried out with two models for each of the four species. In addition to the original model, we applied a modified model that assumed the rate of rest break to be at the maximal level modelled for $+5^\circ\text{C}$ in all air temperatures below $+5^\circ\text{C}$ as well. In other words, in Eqs. (7) and (8) in Table 2, the third formula presented for the range $+5^\circ\text{C} \leq T < +15^\circ\text{C}$ was applied to all temperatures $T < +5^\circ\text{C}$ also (see Fig. 2 in the Results Section). We made use of the daily temperature records from Hangzhou, southeastern China ($30^\circ08\text{N}$, $120^\circ06\text{E}$) for 1958–2018. The hourly temperature data needed in the simulations was not available in the temperature record, which is why the hourly temperatures were generated from the daily temperature data following Zohner et al. (2020) (Eq. (13) in Table 2).

2.6. The software used in the study

Most of the data analyses and model calculations were carried out

with R statistical software v.4.0.2 (R Development Core Team, 2020). The sensitivity analyses were done with source codes written in Fortran with the Visual Studio 2010 software.

3. Results

3.1. Process-based spring phenology models for the four subtropical tree species

For *Pseudolarix* and *Torreya*, the experimental results for Sub-model I show a clear decrease in the rate of rest break at temperatures from $+5^\circ\text{C}$ to $+15^\circ\text{C}$ (Fig. 2c and d). Accordingly, for that measured temperature range, the temperature response of the rate of rest break for these two species is represented by a descending line (Fig. 2c, d and Table 5). In *Castanopsis*, a plateau response over the measured temperature range was found, and accordingly, a horizontal line was used in the curve fitting for the model formulation (Fig. 2a and Table 5). A similar plateau response was assumed for *Phoebe*, despite an outlier observed at $+15^\circ\text{C}$ (Fig. 2b and Table 5). In the absence of experimental results at the low and the high end of the temperature range, the rate of rest break for all four species was a priori assumed to decrease to zero at the temperature ranges from $+5^\circ\text{C}$ to -3.4°C and from $+15^\circ\text{C}$ to $+20^\circ\text{C}$ (Fig. 2 and Table 5).

For the air temperature response of the potential rate of ontogenetic development, $R_{o,pot}$, addressed by Sub-model II, the sigmoidal equation fitted to the results for all four species quite well in general (Fig. 3 and Table 6). In the estimated air temperature response of $R_{o,pot}$, there were marked differences between the species (Fig. S5). For *Castanopsis*, *Phoebe*, and *Torreya*, the lower temperature threshold for ontogenetic development was estimated to be approximately $+10^\circ\text{C}$, whereas for *Pseudolarix*, the rate of ontogenetic development was estimated to be considerable at temperatures below $+10^\circ\text{C}$ also (Figs. 3 and S5). For *Torreya* seedlings, the curve was estimated to level off at $+20^\circ\text{C}$ already, and their rate of development was also estimated to be generally lower than that of the seedlings of the other species. For *Castanopsis*, *Phoebe*, and *Pseudolarix*, the curve levelled off near $+30^\circ\text{C}$ (Figs. 3 and S5).

Considerable differences were found between the four species in the estimated dependence of ontogenetic competence, C_o , on the state of rest break, S_r , addressed by Sub-model III (Fig. 4 and Table 7). In broad

Table 5

Parameter values of Sub-model I (Eqs. (7) and (8) in Table 2) for seedlings of each of the four tree species examined. Sub-model I represents the air temperature response of the rate of rest break, R_r (Fig. 2). Parameter k_2 was not estimated for *Castanopsis* and *Phoebe*.

Tree species	Parameter					
	k_1	k_2	k_3	d_1	d_2	d_3
<i>Castanopsis sclerophylla</i>	0.0077	–	–0.0130	0.0263	0.0650	0.2600
<i>Phoebe chekiangensis</i>	0.0183	–	–0.0308	0.0623	0.1540	0.6160
<i>Pseudolarix amabilis</i>	0.0094	–0.0039	–0.0080	0.0319	0.0984	0.1596
<i>Torreya grandis</i>	0.0150	–0.0062	–0.0127	0.0509	0.1567	0.2548

Table 6

Parameter values of Sub-model II (Eq. (10) in Table 2) for seedlings of each of the four tree species examined. Sub-model II represents the sigmoidal air temperature response of the potential rate of ontogenetic development, $R_{o,pot}$ (Fig. 3). The potential rate of ontogenetic development indicates the rate after rest completion, when there is no longer any reduction of the rate caused by the rest status of the bud. The parameters a_2 , b_2 , and c_2 indicate the upper asymptote (maximal rate), steepness, and inflection point of the sigmoidal curve, respectively.

Tree species	a_2 (% h ⁻¹)	b_2 (°C ⁻¹)	c_2 (°C)	R ²
<i>Castanopsis sclerophylla</i>	0.3984	-2.9868	20.0907	0.8518
<i>Phoebe chekiangensis</i>	0.3451	-3.6026	20.5672	0.9041
<i>Pseudolarix amabilis</i>	0.3008	-3.6984	14.4639	0.6125
<i>Torreya grandis</i>	0.1130	-1.8091	17.2439	0.9401

terms, two patterns are seen in the results. First, in *Pseudolarix* (Fig. 4c) and *Torreya* (Fig. 4d), C_o stays at zero with low values of S_r but gets positive as soon as S_r reaches about 25%. At that point, the zero value of C_o changes abruptly into a positive one, indicating that half of the seedlings showed leafout with the corresponding chilling duration (see Eq. (11) in Table 2). After that, C_o increases continuously with increasing values of S_r in these two species. Second, in *Castanopsis* (Fig. 4a) and *Phoebe* (Fig. 4b), C_o has a positive value even at $S_r = 0\%$, indicating that in these two species leafout can take place even without chilling. Considerable differences between the four species were also found in the slope of the dependence of C_o on S_r (Fig. 4 and Table 7).

3.2. Tests of the models with independent leafout data and the dormancy dynamics predicted by the models

The dormancy dynamics predicted for one overwintering season on our campus is shown in Fig. 5. In all species, rest break was predicted to start at the beginning of the simulation on November 23, as indicated by the increasing values of the state of rest break, S_r (Fig. 5b–e). This was because at the time, the air temperature was mainly fluctuating within

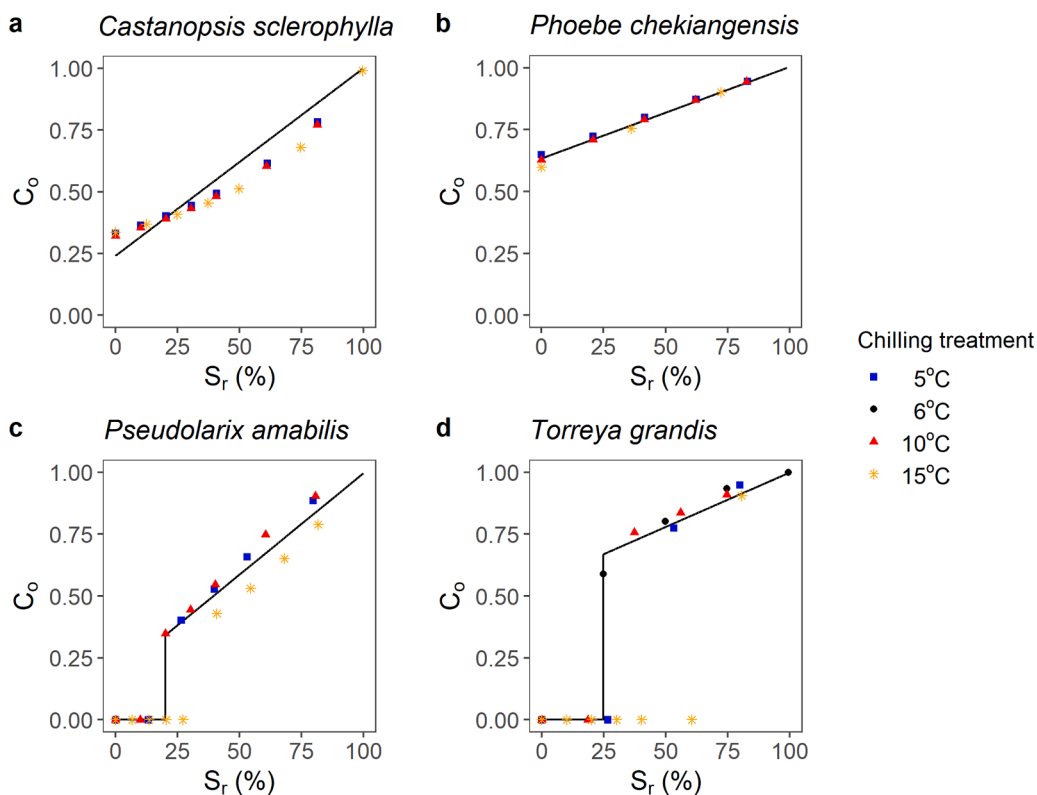


Fig. 4. Sub-model III for each of the four tree species examined, representing the dependency of ontogenetic competence, C_o , on the state of rest break, S_r , (function f_3 in the overall model, Fig. 1). The data points were determined on the basis of the experimental results of Zhang et al. (2021a). Function f_3 is formulated according to Eq. (12) (Table 2) with the parameter values presented in Table 7. The value of S_r indicates the percentage of the physiological changes of rest break caused by chilling and required for rest completion that have taken place at a given moment. The value of C_o indicates the relative effect of the rest condition on the rate of ontogenetic development. With $C_o = 0.5$, for instance, twice as much time is required for leafout as is required after rest completion ($S_r = 100\%$) with $C_o = 1$.

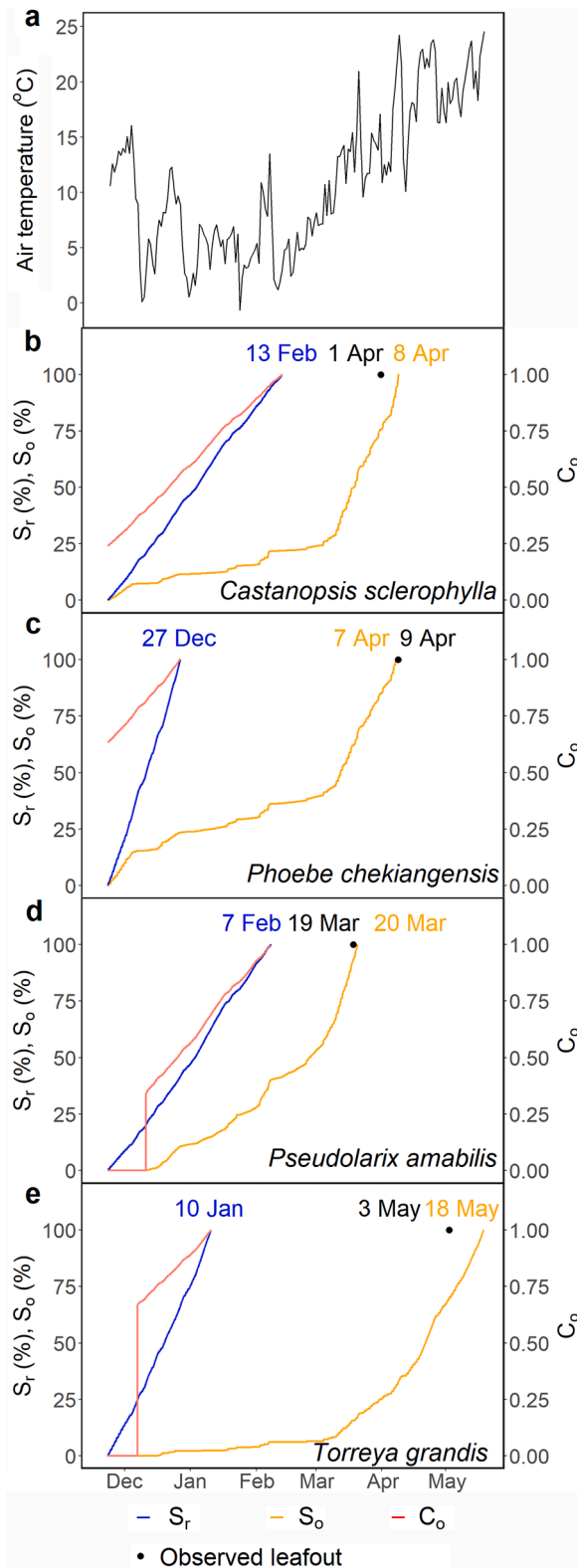
the rest-breaking range already (Fig. 5a; compare with Fig. 2). Rest break was the fastest in *Phoebe* seedlings, where rest completion was predicted to occur on 27 December (Fig. 5c). This is because *Phoebe* seedlings retain their high rate of rest break over a broad temperature range (Fig. 2b). In the other species, the rest completion date varied from 10 January in *Torreya* (Fig. 5e) to 13 February in *Castanopsis* (Fig. 5b).

Besides the predicted S_r , the rate of ontogenetic development is also affected by two other phenomena. First, there are differences between the species in the dependence of ontogenetic competence, C_o , on S_r (Sub-model III; Fig. 4). Thus, contrary to *Pseudolarix* (Fig. 5d) and *Torreya* (Fig. 5e) seedlings, *Castanopsis* (Fig. 5b) and especially *Phoebe* (Fig. 5c) seedlings showed considerable predicted ontogenetic development as early as the first weeks of the simulation, despite the relatively non-progressed rest break in all four species, as indicated by their low values of the state of rest break, S_r , at the time. This is because unlike *Pseudolarix* (Fig. 4c) and *Torreya* (Fig. 4d), *Castanopsis* (Fig. 4a) and especially *Phoebe* (Fig. 4b) already have considerable ontogenetic competence at the beginning of the rest period with $S_r = 0\%$. Second, even when two species have the same C_o , there may be differences in their rate of ontogenetic development because of differences in Sub-model II (Fig. 3). *Torreya* seedlings, for instance, show an exceptionally low rate of ontogenetic development (Fig. S5), and accordingly,

Table 7

Parameter values of Sub-model III (Eq. (12) in Table 2) for seedlings of each of the four tree species examined. Sub-model III mediates the effect of the rest status on the rate of ontogenetic development towards bud burst by formulating the dependence of ontogenetic competence, C_o , on the state of rest break, S_r (Fig. 4).

Tree species	Parameter	
	a_3	$S_{r,min}$
<i>Castanopsis sclerophylla</i>	0.0076	0
<i>Phoebe chekiangensis</i>	0.0037	0
<i>Pseudolarix amabilis</i>	0.0082	20.16
<i>Torreya grandis</i>	0.0044	24.85



(caption on next column)

Fig. 5. A simulation illustrating the dormancy dynamics predicted by the models developed in the present study. (a) Daily mean temperatures for the campus seedling collection. (b–e) Predicted dormancy dynamics for autumn 2018 and spring 2019 of each of the four tree species examined. The vertical axis on the left represents the state of rest break, S_r , (blue line) and the state of ontogenetic development, S_o , (orange line). Rest completion is predicted to occur when $S_r = 100\%$ (date marked in a blue font) and leafout when $S_o = 100\%$ (date marked in an orange font). The observed leafout is marked with a circle and the date in a black font. The vertical axis on the right represents ontogenetic competence, C_o , (red line). By definition, $C_o = 1$ at rest completion, when $S_r = 100\%$. Otherwise the relationship between C_o and S_r varies amongst the four tree species as shown in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

despite their earlier rest completion in comparison with *Pseudolarix* and *Castanopsis* seedlings, the predicted ontogenetic development of *Torreya* seedlings soon fell behind that of the seedlings of the other two species (Fig. 2b, d and e).

In predicting the timing of spring phenology, the highest accuracy in this limited short-term test based on spring 2019 observational data was reached with *Pseudolarix*, where the prediction was one day late (Fig. 5d). *Pseudolarix* was followed by *Phoebe* (two days early, Fig. 5c), *Castanopsis* (seven days late, Fig. 5b), and *Torreya* (fifteen days late, Fig. 5e).

The results of the main tests of the models are shown in Fig. 6. The model developed for *Torreya* provided relatively accurate predictions for the timing of leafout in seedlings in the warming WTC experiment of the present study (Fig. 6d). For *Torreya*, the predictions were also unbiased. In comparison with *Torreya*, the accuracy reached with the other three species was lower (Fig. 6a–c). Additionally, a bias was introduced into the model predictions for *Phoebe* (Fig. 6b) and *Pseudolarix* (Fig. 6c): the predicted leafout times were systematically earlier than the observed ones. No clear difference between the test with the phenological records and the test with the warming experiment was found for any of the three species where data was available for both (Fig. 6a–c). This was the case despite the fact that the phenological records represent leafout in mature trees whereas the models were developed on the basis of experiments with seedlings.

3.3. Sensitivity analysis

In *Torreya*, *Phoebe*, and *Castanopsis* seedlings, a negligible sensitivity to the difference represented by the two alternative models used as Sub-model I (Fig. 2) was found. The percentage of the years with a difference in the timing of bud burst found between the two alternative sub-models in *Torreya*, *Phoebe*, and *Castanopsis* seedlings was 1.6%, 6.6%, and 19.7% respectively, but in all years where there was a difference, the modified model predicted bud burst to occur only one day earlier than the original model (Table 8). *Pseudolarix* seedlings showed a higher sensitivity, with a difference between the predictions of the alternative models appearing in 77% of the years. Between the results obtained with the two alternative sub-models, the average difference was 1.9 days and the maximum difference 7 days (Table 8).

4. Discussion

4.1. Ecophysiological approach to process-based modelling of tree phenology

We introduced novel process-based models of spring phenology for four subtropical tree species. As predicted in our hypothesis, the process-based models developed on the basis of explicitly designed experiments showed considerable differences in the dormancy phenomena between the subtropical tree species examined (Figs. 2–5). We examined only four subtropical tree species, so that further studies with additional

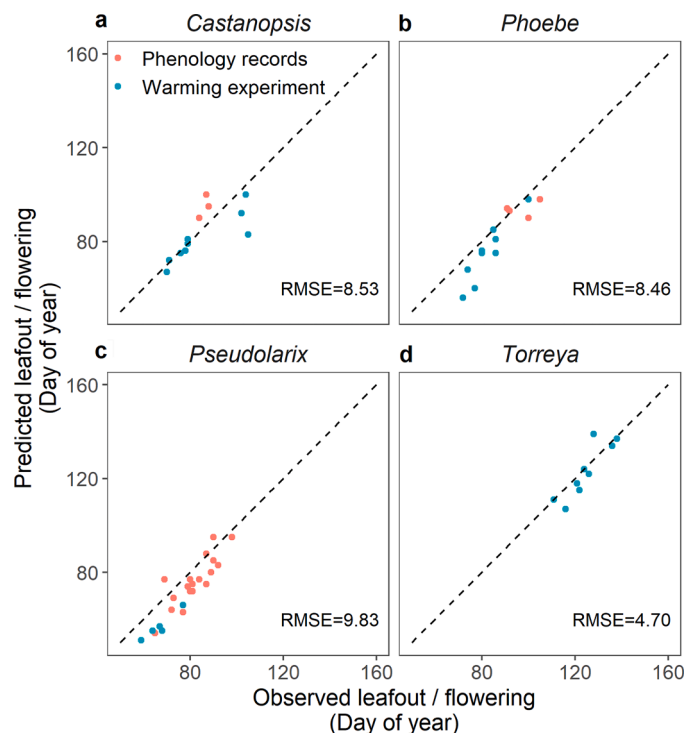


Fig. 6. Independent tests of the process-based spring phenology models developed for the four subtropical tree species in the present study. The models were tested by using both phenological records and results from our warming whole-tree chamber (WTC) experiment. The phenological records represent leafout in mature trees, whereas the results from the WTC experiment represent leafout in the seedlings. The predictions for the phenological records of *Castanopsis*, *Phoebe*, and *Pseudolarix* trees were calculated by means of the models developed for seedlings because no model for mature trees was developed in the present study. No phenological records of leafout in mature trees were available for *Torreya*.

Table 8

Results of the sensitivity analysis of the potential rest-breaking effects of temperatures below +5 °C on the timing of bud burst in the subsequent spring. The timing of bud burst in Hangzhou, southeastern China, was simulated for 61 years by using two alternative models for the temperature response of rest break. In the original model, no rest break was assumed to take place at temperatures below -3.4 °C, whereas in the modified model, rest break was assumed to progress at its maximal rate at all temperatures below +5 °C (Fig. 2). The mean difference reported in the table is for the years when there was a difference in the prediction between the two models. The positive values of the difference indicate that the modified model predicted an earlier bud burst than the original model.

Material category	Percentage of years with a difference in the prediction	Mean difference (days)	Maximal difference (days)
<i>Castanopsis</i> seedlings	19.7	1	1
<i>Phoebe</i> seedlings	6.6	1	1
<i>Pseudolarix</i> seedlings	77.0	1.9	7
<i>Torreya</i> seedlings	1.6	1	1

species are called for in order to examine how common such interspecific variation is in the subtropical forests of south-eastern China. Note, however, that the differences found in the present study between the four species would have been improbable if such interspecific variation were not common.

The main emphasis in our modelling was on the biological realism of the models (Levins, 1966, 1968; Charrier et al., 2015; Hänninen, 2016), which is why we took an experimental approach explicitly addressing the air temperature responses modelled. The models developed on the basis of experimental studies predicted the timing of leafout in independent data sets not used for model development with reasonable accuracy. This approach, referred to as the ecophysiological approach by Hänninen (2016), has been taken with boreal and temperate trees only rarely (Sarvas, 1972, 1974; Campbell and Sugano, 1975, 1979; Caffarra et al., 2011) and, to our knowledge, with subtropical trees never before. The obvious reason for the shortage of earlier studies is the large amount of labour required by the experiments (Baumgarten et al., 2021).

The modular model structure adopted in the present study (Fig. 1) facilitates the designing of particular experiments with each one addressing a specific ecophysiological response that affects the timing of the spring phenological event. The modular model structure was introduced as early as 30 years ago (Hänninen, 1990), but as far as we know, our study is the first one to use it to its full potential, basing all three sub-models on specific experimental data for the species addressed. To facilitate that, we introduced a novel methodological framework. Actually, the methods we used for Sub-models I and II had been introduced several decades ago (Sarvas, 1974; Campbell, 1978), but for Sub-model III a novel method was needed; and, most importantly, we combined the methods for all three sub-models into one framework. The framework developed in the present study can be applied to developing biologically realistic process-based tree phenology models for all tree species that show the phenomena of rest (endodormancy) and chilling requirement, no matter whether the trees are boreal, temperate, or subtropical.

The concept of ontogenetic competence introduced by Hänninen (1990) is essential in the modular model structure adopted in the present study (Fig. 1). It explicates a phenomenon that is addressed implicitly by using a priori assumptions in the classic two-phase models (sequential and parallel), including both chilling and forcing effects. In the sequential model, it is assumed that the ontogenetic development (forcing) starts only after the chilling requirement has been met (Hänninen, 1987, 2016). This is a strong assumption and has little if any explicit experimental support. Still, the sequential model is used quite often, probably because of its simplicity (Hänninen, 1991; Kramer, 1994; Chuine et al., 1998; Linkosalo et al., 2006; Fu et al., 2012; Basler, 2016). In our explicit approach the sequential model would be represented by a Sub-model III having the value of $C_0 = 0$ with $S_r < 100\%$ and $C_0 = 1$ with $S_r = 100\%$ (Hänninen, 1990, 2016). Our experimental results show that none of the four species examined in the present study showed that kind of response. Rather, *Castanopsis* and *Phoebe* showed a gradually increasing C_0 with increasing S_r (Fig. 4a and b) as implied by the parallel model (Hänninen, 1990, 2016), whereas *Pseudolarix* and *Torreya* showed an intermediate response (Fig. 4c and d) representing a model intermediate between the two classical two-phase models (Hänninen, 1990, 2016). When the explicit Sub-model III is determined on the basis of experimental data, no a priori assumptions about the phenomenon modelled are needed. Similar flexibility was introduced ten years later into the unifying model (Chuine, 2000), and recently into the PhenoFlex model also (Luedeling et al., 2021). In both of them, a novel mathematical formalism was applied instead of the one based on the concept of ontogenetic competence (Hänninen, 1990). Out of these three optional approaches we adopted the approach of Hänninen (1990) because it has an explicit concept for the physiological phenomenon addressed (ontogenetic competence) and because it also facilitates the graphical explication of the phenomenon addressed (Fig. 4).

The ecophysiological approach based on experimental work was adopted early on by Fishman et al. (1987a, b). They developed a process-based rest break model, which is fundamentally different from all other models developed before and after their work. While the other models of rest break simulate it as a homogeneous process (Sarvas, 1977), the model of Fishman et al. (1987a, b) simulates it as a two-step

process, where the rest-breaking effect of chilling is reversed initially by potential exposure to subsequent high temperatures but consolidated at the next step if no such high temperatures occur (Cannell, 1989; Pitacco, 1990). The model was able to reproduce many experimental findings under various fluctuating temperature conditions, including chilling negation under high temperatures. Subsequently, the model has become a standard reference in process-based tree phenology modelling under the name 'Dynamic Model' (Pitacco, 1990; Luedeling et al., 2009, 2021; Xu et al., 2020; Egea et al., 2021). That name might actually be misleading, for according to the standard terminology of general systems theory, all process-based tree phenology models are dynamic (Hänninen, 2016). By now, however, the name 'Dynamic Model' has become established, probably because it emphasizes the complicated dynamics of the two-step process assumed. It should be noticed that the 'Dynamic Model' can be readily introduced, as a Sub-model I, into the modular overall model adopted in the present study (Fig. 1; Hänninen and Kramer, 2007). However, as no experimental evidence for the high temperature negation of rest break has been shown for subtropical trees so far, the 'Dynamic model' was not applied in the present study.

Process-based tree phenology models aim at addressing the actual physiological and morphological processes taking place in the buds (Hänninen et al., 2019). However, this essential starting point of the modelling may be obscured by the fact that the state variables of the models, state of rest break (state of chilling, Kramer, 1994; Chuine et al., 1998) and state of ontogenetic development (state of forcing, Kramer, 1974; Chuine et al., 1998), are usually not tested against observations and measurements of the corresponding real phenomena in the trees. Rather, as exemplified by the present study, a hypothetico-deductive approach is taken where the non-observed phenomena are modelled by the implications their air temperature responses have for the occurrence and timing of bud burst, which are readily observable (Sarvas, 1974; Campbell, 1978). For this reason, it may be argued that a less ambitious attribute, such as 'process-orientated model' (Archetti et al., 2013), would describe the approach better than the concept 'process-based model.' However, as the concept 'process-based model' is firmly established (Chuine and Régnière, 2017; Hänninen et al., 2019), changing it would confuse rather than clarify communication about the modelling approach taken.

The biological realism of process-based tree phenology modelling would be considerably improved if there were direct physiological and molecular data for testing the predicted values of the model variables (Luedeling et al., 2021). For instance, what happens in the buds when the value of the state of rest break increases from 0 to 100% during autumn and winter (Fig. 5)? Or which molecular and physiological phenomena explain our finding that in the different species, a given state of rest break corresponds to different ontogenetic competences (Fig. 4), leading to different timings of bud burst? Even though the ecophysiological HDM approach cannot answer these questions by itself, it helps in identifying and framing these research questions for studies at the cellular, physiological and molecular levels. As a perspective for the improvement of the biological realism of budburst models (Hänninen, 2016), we call for a combination of the ecophysiological approach carried out at the whole-tree level, as exemplified by the present study, and physiological approaches carried out at the cellular and molecular levels (Rinne et al., 2011; Cooke et al., 2012; Kudoh, 2016; Singh et al., 2017; Tylewicz et al., 2018; Beauvieux et al., 2018).

4.2. Other approaches to process-based tree phenology modelling

In the process-based modelling of the spring phenology of trees, an approach partially based on previous experimental findings is sometimes taken. In this approach, referred to as the intermediate approach by Hänninen (2016), rest break is simulated by accumulating chilling units and ontogenetic development by accumulating forcing units. Both simulations use temperature responses previously determined experimentally for some other species than the ones being modelled. In that

approach, only the chilling and forcing requirements are determined on the basis of species-specific data (Häkkinen et al., 1998; Luedeling et al., 2009; Xu et al., 2020). With reference to the temperature responses determined in the present study (Figs. 2 and 3), this would mean that the shape of the temperature response curve is fixed a priori but the level is estimated from new species-specific data: the higher the chilling/forcing requirement, the lower the level of the corresponding curve (Hänninen, 2016).

Our explicit experimental results show that there are considerable differences between the examined four subtropical tree species in their air temperature responses of the rate of rest break (Fig. 2) and ontogenetic development (Fig. 3). Even bigger differences were found between our results for the subtropical trees and those found earlier for boreal and temperate trees. Most importantly, we found that temperatures of up to +15 °C are effective in the rest break of many subtropical tree species. In fact, we were not even able to determine the upper limit of the rest-breaking temperature range for the subtropical tree species we studied (Zhang et al., 2021a) and therefore made a hypothesis that this upper limit exists and has the value of +20 °C (Fig. 2). In most of the previous experimental studies of more northern trees, the upper threshold was found to be +10 to +12 °C or lower (Sarvas, 1974; Heide and Prestrud, 2005, however, see Erez and Couvillon, 1987; Harrington et al., 2010). Similarly, we found in the present study that temperatures between 0 and +10 °C, which have been found to promote ontogenetic development towards bud burst in boreal and temperate trees (Sarvas, 1972), are ineffective for many subtropical trees. Along this same line of reasoning, Baumgarten et al. (2021) recently found considerable differences between six temperate tree species in their air temperature responses of the rate of rest break. All of these comparisons indicate that there is no chilling unit for rest break and no forcing unit for ontogenetic development based on response curves fixed a priori that could be universally valid for all species. Rather, modelling needs to be based on species-specific or possibly even provenance-specific data (Hänninen, 2016; Kramer et al., 2017; Baumgarten et al., 2021).

In seeking to attain species-specific models, an approach referred to as the phenological approach by Hänninen (2016) is often taken. In this approach, process-based tree phenology models are developed with the technique of inverse modelling, which means that rather than basing the models and their parameter values on experimental studies explicitly designed to examine the air temperature responses involved, the models and their parameter values are determined by fitting the models statistically to observational long-term phenological records (Kramer, 1994; Chuine et al., 1998; Basler, 2016). The approach has become popular since it requires no experimental work and long-term phenological records are nowadays readily available for several tree species and geographical locations. However, as already shown by the pioneering study of Hunter and Lechowicz (1992), inverse modelling involves an exceptionally high degree of uncertainty and often produces biologically unrealistic models, as discussed recently by Hänninen et al. (2019). Accordingly, when developing the first process-based model for a subtropical tree species, Chen et al. (2017) used the inverse modelling framework. Unfortunately, their study, too, was undermined by unrealistic temperature responses of chilling accumulation (Fig. S6).

Recently, the methodological problem involved in inverse modelling was encountered by Luedeling et al. (2021). With the aim to solve many of the problems that have hindered the progress of process-based modelling of tree phenology, they introduced a novel flexible process-based model called PhenoFlex. They applied a set of sophisticated modelling techniques, achieving many of their goals. For instance, Luedeling et al. (2021) used observational air temperature and phenological records for 1959 – 1998 for training their models and similar records for 1999 – 2018 for testing them. The latter period was warmer than the former, and thus the use of the two time periods separately allowed Luedeling et al. (2021) to improve the robustness of the models by testing them under conditions which were not used for their calibration. However, despite all the advances, their modelling analysis

ended up in the unrealistic result of +30 °C being a rest breaking chilling temperature in temperate apple trees. As discussed by the authors, that unrealistic assumption was caused by the fact that temperatures above +10 °C occurred only rarely in the observational training data set (Luedeling et al., 2021). This discussion demonstrates, once again, the fundamental methodological problem inherent in inverse modelling. The problem cannot be solved by further improvements of the methods used in the analysis of the observational data, for the problem is the insufficient information provided by the data. That is the very reason why experimental research is needed in the development of realistic process-based models of tree phenology (Hänninen et al., 2019; Egea et al., 2021).

4.3. Further model development

Though our experimental approach explicitly addressed the responses being modelled, the models developed still require further work for better biological realism. Several additional aspects need to be addressed in further work of process-based modelling for subtropical trees. The most obvious one is seen in Fig. 2, which shows that in the sub-model for the air temperature response of the rate of rest break, a priori assumptions were generally needed at both the low and the high end of the temperature spectrum. However, when experiments are carried out to add the missing data points, various methodological problems come up. Temperatures above +15 °C generally cause ontogenetic development towards bud burst, thus lowering the value of DBB and confusing the determination of the chilling duration required for rest completion. At the lower end of the temperature scale, problems may be met in chilling with freezing temperatures because subtropical tree species do not necessarily survive in continuous freezing conditions (Zhang et al., 2021a). The sensitivity analyses also suggest that temperatures below +5 °C occur at the subtropical research site so rarely that their effect on rest break may be quite limited with most species. Still, at least the temperatures between zero and +5 °C need to be studied for their rest-breaking effects. Lastly, it should be noted in any evaluation of the present temperature responses of the rate of rest break that in the mainline approach of using inverse modelling based on observational leafout data, no observations of rest break are available (Kramer, 1994; Chuine et al., 1998; Basler, 2016). Thus even rest break models based on experiments with a single controlled temperature (Lundell et al., 2020; Zheng et al., 2021) have a more solid empirical basis than those based on inverse modelling.

In addition, the effects of fluctuating temperatures (Fishman et al., 1987a, b; Hänninen, 2016) and of photoperiod on rest break (Zhang et al., 2021b) need to be introduced into the process-based modelling for subtropical trees. Furthermore, the post-rest theory introduced by Vegis (1964) and recently formulated for boreal field layer plants by Lundell et al. (2020) should be examined with reference to subtropical trees, too. The theory suggests that the temperature range promoting ontogenetic development changes during dormancy. That change provides a potential explanation for the bias of the model prediction observed in the present study with two species in the independent test (Fig. 6; Hänninen, 2016). The generic concept of ontogenetic competence (Fig. 1) used in the present study was also used by Lundell et al. (2020), showing that the concept can be applied in a broad range of studies where restrictions caused by the rest status on the ontogenetic development need to be addressed.

5. Conclusions

We developed process-based models of spring phenology for four subtropical tree species. The development of the models was based entirely on specific experiments designed to address the three temperature responses, one at a time, that affect the spring phenology. For the model development, a methodological framework for combining the experimental work with the modelling was introduced. Mostly,

reasonable accuracy was attained in testing the models with independent data, both observational and experimental. The experimental results showed considerable differences between tree species in the temperature responses of the dormancy processes addressed by the models, and these differences had major implications for the dormancy dynamics predicted by the models. These findings show the power of the experimental approach and, at the same time, calls for further experimental studies, our study being the first of its kind. The framework developed in the present study can be applied to developing biologically realistic process-based tree phenology models for all tree species that show the phenomena addressed in the framework, i.e., rest (endodormancy) and chilling requirement, no matter whether the trees are boreal, temperate, or subtropical.

Declaration of Competing Interest

None

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.agrformet.2021.108802](https://doi.org/10.1016/j.agrformet.2021.108802).

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