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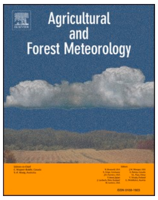

Research paper

Differences between four sympatric subtropical tree species in the interactive effects of three environmental cues on leaf-out phenology

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ABSTRACT

Climatic warming is currently changing the spring phenology of extratropical trees, and this has several important effects on the trees and ecosystems. The major climatic cues regulating the spring phenology are winter chilling, spring forcing, and photoperiod. The interactions between these three remain largely unstudied because most studies concentrate on the effects of one cue, or maximally two, at a time. We studied the effects and interactions of chilling duration, forcing temperature, and forcing photoperiod simultaneously in four subtropical tree species. The main emphasis in our experiments was on the interaction of chilling duration and forcing temperature. The existence of this interaction was suggested in the 'Vegis theory', put forward decades ago but largely forgotten since. We also introduced a novel method for testing the theory experimentally. We found support for the Vegis theory in two of the four species examined. In the other two species the leaf-out timing was largely controlled by spring forcing. The effects of photoperiod were generally minor. Our results show that there are major differences between sympatric subtropical tree species in their phenological responses to environmental cues. These differences need to be addressed in the development of process-based tree phenology models. Our results further suggest that different subtropical trees respond differently to climatic warming because of differences related to the Vegis theory. This hypothesis remains to be tested in further studies.

1. Introduction

The spring phenology of perennial plants is critical for the functioning of terrestrial ecosystems and ultimately for the global cycling of carbon (Richardson et al., 2009). During the last few decades, spring leaf-out has accelerated as a result of the global warming (Chuine et al., 2000; IPCC, 2014), though it has also been found that the temperature sensitivity of leaf phenology has recently declined in some cases (Fu et al., 2015). Assessing the future effects of climatic warming on the spring phenology of trees is crucial, for these effects not only are important for the survival, growth and reproduction of trees but also scale up to impacts on ecosystem productivity and carbon cycling (Wang et al., 2019). Unfortunately, the current tree phenology models are not yet realistic and accurate enough for projecting tree phenology under climatic warming (Wang et al., 2020a), so that further experimental studies are needed to improve our understanding of the effects of climatic cues on the spring phenology of trees (Flynn and Wolkovich, 2018; Hänninen et al., 2019).

The occurrence of spring leaf-out in boreal and temperate trees is the result of two major dormancy processes that occur over a prolonged time, starting in the previous autumn. First, leaf-out is prevented during autumn and winter endodormancy by growth-arresting physiological conditions inside the bud (Fuchigami et al., 1982; Lang et al., 1987). These conditions are removed mainly by the accumulation of low chilling temperatures (Fuchigami et al., 1982). After that, the trees are in the state of ecodormancy, so that their leaf-out is prevented solely by the low air temperatures typically occurring at that time of the year (Hanninen, 2016). In this phase, high forcing temperatures are required for ontogenetic development, i.e., the microscopic anatomical development in the buds, which finally leads to the occurrence of visible

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leaf-out (Lang et al., 1987; Basler and Körner, 2014).

The effects of chilling and forcing temperatures on the spring phenology of temperate trees are well-established for boreal and temperate trees (Way and Montgomery, 2014; Delpierre et al., 2016; Flynn and Wolkovich, 2018) and more recently, for subtropical trees as well (Du et al., 2019; Song et al., 2020; Zhang et al., 2021a). There is a well-known interaction of chilling and forcing, where the amount of forcing required for leaf-out declines exponentially with increased previous chilling accumulation (Harrington and Gould, 2015; Fu et al., 2015; Wang et al., 2020b; Zhang et al., 2021a). Thus insufficient chilling accumulation during autumn and winter may delay or even prevent the spring leaf-out because of incomplete endodormancy release (Petri and Leite, 2004).

According to Vegis (1964), the interaction of chilling and forcing temperatures in determining the spring phenology is more complex than the exponential decline of the amount of forcing required for leaf-out with increased chilling. Vegis (1964) put forward a generalized theory suggesting that the changes taking place during endodormancy release are more profound. Accordingly, the growth-promoting temperature range changes along with changes in the dormancy status of the plants. In trees evincing endodormancy and a chilling requirement, this means that the lower threshold temperature allowing leaf-out decreases when dormancy is released as a result of accumulation of chilling (Hänninen, 1990). Vegis' (1964) theory has been addressed frequently in seed dormancy studies (Vegis, 1964; Junttila, 1970), but in bud dormancy studies it has remained largely forgotten. This is unfortunate, for the phenomenon suggested by Vegis (1964) may have crucial implications for the effects of climatic change (Hänninen, 2016). Junttila & Hänninen (2012), however, found support for the theory with *Betula pendula* and *B. pubescens* seedlings: the seedlings required higher forcing temperatures for leaf-out after a short duration of chilling than after a long one.

Vegis' (1964) original theory addresses the categorical question of whether or not leaf-out is observed in a given forcing temperature. For brevity's sake, this phenomenon will be referred to here as the *Vegis occurrence effect*. Lundell et al. (2020) broadened the scope of the theory to cover the rate of development towards leaf-out. According to this second effect, the difference in the rate of development between a low and a high forcing temperature is large after a short duration of chilling and decreases with additional chilling accumulation. Accordingly, the forcing temperature has a large effect on the rate of development after a short duration of chilling, but the effect decreases with prolonged chilling. Rather than affecting the occurrence of leaf-out, the rate of development affects its timing; so, this second effect will be referred to here as the *Vegis timing effect*. On the basis of their experimental results, Lundell et al. (2020) concluded that five out of the seven boreal plant species examined showed the Vegis timing effect.

Contrary to the studies of the effects of chilling and forcing, there are fewer studies of the role of photoperiod in regulating the spring phenology of trees, and that role remains to be debated (Chuine et al., 2010; Körner and Basler, 2010; Fu et al., 2019b; Meng et al., 2021). In many tree species, an interaction of photoperiod and chilling is observed, as long photoperiods compensate for lack of chilling in non-chilled or partially chilled trees but have no effect after the chilling requirement has been met (Myking and Heide, 1995; Caffarra and Donnelly, 2010; Meng et al., 2021; Zhang et al., 2021b). However, there is also increasing evidence for an independent role of photoperiod in regulating the endodormancy release and leaf-out in many temperate (Zohner and Renner, 2015; Singh et al., 2016; Fu et al., 2019a; Meng et al., 2021) and subtropical (Zhang et al., 2021b) tree species. In most boreal trees, leaf-out seems to show little sensitivity to photoperiod (Zohner et al., 2016; Richardson et al., 2018).

Due to practical limitations, mainly concerning labor and growth chamber facilities, experimental studies on the environmental regulation of tree spring phenology have usually been carried out by simultaneously addressing only one, or maximally two, of the three major environmental cues (chilling, forcing, photoperiod) that regulate spring phenology. In particular, the two Vegis effects have been studied only rarely because studies addressing the effects of chilling usually apply one standard forcing temperature only. This is unfortunate, for this limited approach disallows the finding of potential interactions among the three factors (Ettinger et al., 2020). Here we examined the effects of the three climatic cues on leaf-out in four subtropical tree species simultaneously. The experimental seedlings and twigs were first exposed to varying durations of chilling at +6°C and then to six combinations of three forcing temperatures and two forcing photoperiods. This allowed us to examine not only the effects of each of the three factors but also their interactions. Our main emphasis was on the two Vegis effects, previously almost unaddressed. To that end, we introduce a novel method for testing the Vegis timing effect. To the best of our knowledge, neither of the two Vegis effects has been tested with subtropical trees before. Our study provides novel information about the environmental regulation of tree leaf-out in subtropical conditions.

2. Material and methods

2.1. Study site

The study was conducted on the campus of Zhejiang A&F University (30°14′N, 119° 42′E), in Hangzhou, China. The plant materials were obtained from the nearby Tianmushan Forest Station (30°18′N, 119°39′E). The location has a subtropical, monsoonal climate. The mean annual precipitation is 1614 mm, the mean annual air temperature +15.6°C, and the mean monthly air temperature +4.5°C in January and +28.9°C in July (Zhang et al., 2021b).

2.2. Plant material and growth conditions

We examined the effects of the environmental cues on leaf-out in four tree species commonly growing in subtropical south-eastern China: *Castanopsis sclerophylla, Phoebe chekiangensis, Pseudolarix amabilis*, and *Torreya grandis*. Since it is practically impossible to transfer whole trees to growth chambers, seedlings or twigs are commonly used in experimental phenology research (Vitasse and Basler, 2014; Partanen et al., 2016). In our experiments we used first-year seedlings of *Castanopsis, Phoebe,* and *Torreya*. For *Pseudolarix*, twigs detached from mature trees were used since seedlings were not available. *Castanopsis* and *Phoebe* are evergreen broadleaved tree species with leaf-out occurring in early March. *Torreya* is an evergreen conifer species, and its leaf-out occurs in late April. *Pseudolarix* is a deciduous tree species with bud burst occurring in late March. In our experimental site, the air temperature generally drops dramatically in the time window of late November to early December, so that chilling accumulation starts at that time (Zhang et al., 2021b).

Dormant first-year seedlings of *Castanopsis, Phoebe* and *Torreya* were transported from the nursery to our campus on 23 November 2020. The seedlings were transplanted into 2 L polyethylene pots (12*16 cm) filled with a soil substrate containing 5 peat: 2 vermiculite: 1 perlite: 2 organic matter by volume (Universal potting soil, Hangzhou, China). For *Pseudolarix*, approximately 20-cm-long twigs were sampled randomly for the experiments in a *Pseudolarix* plantation. The twigs were detached with scissors from the trees and disinfected with a hypochlorite solution (200 ppm active chlorine). The cut end of each twig was then cut once more in tap water and put in test tubes (3 cm in diameter and 20 cm in height), one twig per tube, with 40 μg L^{-1} of the broad-spectrum antibiotic gentamicin sulfate added (Zohner et al., 2016).

2.3. Experimental design

The experiment was designed to examine the effects of the environmental cues on the two main physiological processes leading to leaf-out, i.e., endodormancy release and ontogenetic development (Fig. 1).

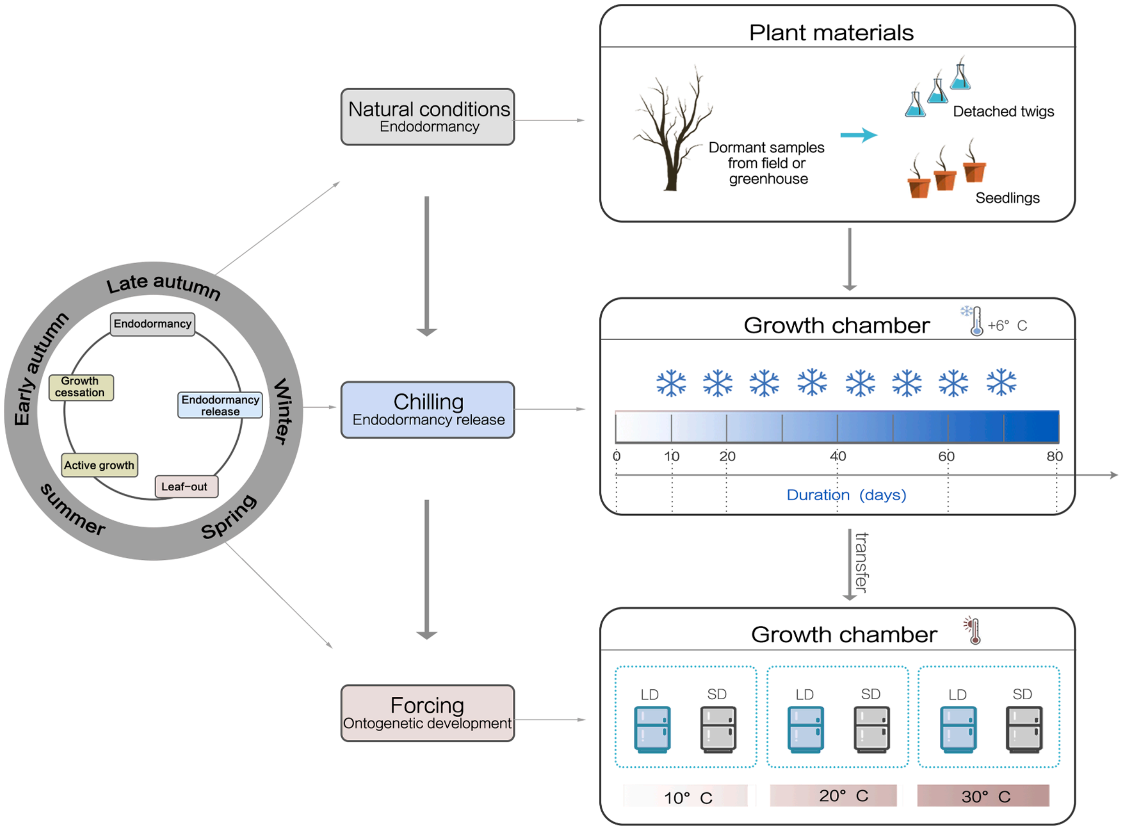

Fig. 1. Experimental design of the study. Dormant seedlings and twigs were sampled in natural conditions on 3 December 2020. The seedlings and detached twigs were first transferred into a chilling treatment at +6°C. After 0–80 days of chilling, a subsample of the seedlings and twigs was transferred from the chilling conditions to each of the six forcing conditions created by combining two photoperiods (SD = 10 h, LD = 14 h) with three air temperatures (+10, +20, and +30°C). In the forcing conditions, a re-growth test was carried out by observing the occurrence and timing of leaf-out.

At the start of the experiment on 3 December 2020 (early winter on the study site), the experimental seedlings and twigs were first put in controlled chilling conditions (+6°C) in growth chambers for endodormancy release, and after 0 – 80 days of chilling accumulation, a subsample of the seedlings and twigs was transferred to each of the six forcing conditions created by combining three air temperatures (10, 20, 30°C) with two photoperiods (SD = 10 h, LD = 14 h) (Fig. 1). In the forcing conditions, a regrowth test was performed by observing the occurrence and timing of leaf-out (see below).

The chilling treatments were implemented in growth chambers (E-Lotus Technology Co., Beijing, China). The relative humidity was 60–75%, photoperiod 10 h, and photosynthetic photon flux density during the light periods 400 μmol $m^{-2}s^{-1}$ (Zhang et al., 2021a,b). The chilling accumulation was varied between the treatment groups by transferring the seedlings/twigs from the chilling conditions to the forcing conditions at six different moments, i.e., after 0, 10, 20, 40, 60, and 80 days of chilling. The six forcing treatments were implemented in corresponding six growth chambers (E-Lotus Technology Co., Beijing, China). The relative humidity was 60–75% and photosynthetic photon flux density during the light periods 400 μmol $m^{-2}s^{-1}$. In order to avoid any systematic effect of the chamber, the six treatments were rotated among the six chambers once every two weeks. Similarly, in order to avoid the effects of any systematic environmental gradients in the chambers, the seedlings and twigs were rotated in each chamber every week. The sample size in each experimental group was ten ($n = 10$), so that for each species, 10 × 6 (durations of chilling) x 3 (forcing temperatures) x 2 (forcing photoperiods) = 360 seedlings/twigs were used. The seedlings were watered once a week in the chilling and the 10°C forcing conditions and every two to three days in the 20°C and 30°C forcing conditions. In order to prevent callusing, the water in the test tubes of the twigs was changed every four to seven days, and every time this was done the cut end of the twig was cut once more under water.

2.4. *Observations of leaf-out*

In the forcing conditions, bud development was monitored every three to four days with a categorical scale of four developmental stages: bud closed, bud swelling, leaf emergence, leaf-out (wrinkled leaves were not considered to reach this stage). The stage of leaf-out of non-wrinkled leaves served as the phenological event to be examined because reaching this stage shows the development is normal, so that cases of abnormal development caused by insufficient chilling were excluded from the analysis of the results. The earlier three stages were observed because observations on them improved the precision of determining the stage of leaf-out (Zhang et al., 2021a). For *Phoebe* and *Castanopsis*, only the terminal buds were observed since these species had no lateral buds. For other species, the timing of bud burst in each seedling/twig was determined by the date when >50% buds reached the last developmental stage, i.e., leaf-out (Harrington and Gould, 2015, Zhang et al., 2021a). The observations of bud burst ended on 9 June, so that they lasted for 188 days from the start of our experiment.

2.5. *Statistical analyses*

For each seedling/twig showing leaf-out, the timing of leaf-out was determined as the days to bud burst, DBB, required for leaf-out in the forcing conditions. Subsequently, for each treatment group (combination of chilling duration, forcing temperature, and forcing photoperiod), the final bud burst percentage, BB%, was used to quantify the occurrence of leaf-out and the mean DBB (±SE) to quantify the timing of leaf-out. (Note that in connection with the standard acronyms BB% and DBB, the generic concept 'bud burst' is used to refer to leaf-out). The differences in BB% between the treatments were analyzed in each of the four species by logistic regression with a binary response (bud burst / no bud burst; Partanen et al., 2016). The differences in DBB among the treatments were analyzed in each of the four species with a three-way analysis of variance (ANOVA) (Partanen et al., 2016). For the response variable, a log transformation of DBB was used. In the analyses of both BB% and DBB, the explanatory variables were the duration of chilling, the forcing temperature, and the forcing photoperiod. The two-way and three-way interactions of the explanatory variables were also examined. All statistical analyses were carried out with the SPSS software (Version 16.0, SPSS Inc., Chicago, USA).

2.6. *Testing the two vegis effects*

The Vegis occurrence effect was tested by the prediction directly implied in its definition (Junttila and Hänninen, 2012): with a short duration of chilling, which does not meet the chilling requirement, the value of bud burst percentage, BB%, is lower for a low forcing temperature than for a high one, but with longer chilling, which meets the chilling requirement, this difference vanishes, so that BB% is at or near 100 % regardless of the forcing temperature (Fig. S1).

For testing the Vegis timing effect (Lundell et al., 2020), a novel method for examining the effect graphically was introduced in the present study. For any given constant forcing temperature T_{forc}, the rate of ontogenetic development towards leaf-out is calculated with the timing of bud burst, i.e., the number of days to bud burst observed in that temperature, $DBB(T_{forc})$ (Campbell, 1978; Hänninen, 2016):

$$R_o\left(T_{forc}\right) = \frac{100}{DBB(T_{forc})} \tag{1}$$

The value of DBB decreases with increasing value of T_{forc}, but also with increased duration of previous chilling, x, implying that the rate of ontogenetic development is a function of both T_{forc} and x:

$$R_o\,(T_{forc}, x) = \frac{100}{DBB(T_{forc}, x)} \tag{2}$$

In the absence of the Vegis timing effect, the rate of ontogenetic development towards leaf-out increases with increasing T_{forc} in relative terms equally with all durations of chilling (Lundell et al., 2020). This implies that the ratio, R, of the rate of development obtained in any two forcing temperatures, $T_{forc\text{-}low}$ and $T_{forc\text{-}high}$, does not depend on the accumulated chilling, x (Supplementary Information Method 1; Fig. S2a). We had three forcing temperatures 10, 20, and 30°C, so that in the absence of the Vegis timing-effect we get:

$$R_{10,20} = \frac{R_o(10, x)}{R_o(20, x)} = c_1 = \text{constant} \tag{3}$$

$$R_{20,30} = \frac{R_o(20, x)}{R_o(30, x)} = c_2 = \text{constant} \tag{4}$$

The values of both c_1 and c_2 are below 1, indicating a higher rate of development at the higher than at the lower temperature.

In the presence of the Vegis timing effect, on the contrary, the rate of ontogenetic development increases with increasing T_{forc} in relative terms more with a short than with a long duration of chilling, x (Lundell et al., 2020). This implies that the ratio R of the rate of development obtained in any two forcing temperatures, $T_{forc\text{-}low}$ and $T_{forc\text{-}high}$, increases when the duration of previous chilling, x, increases from zero, and reaches a constant value (but still <1) with a sufficiently high x (Fig. S2b). So, if the Vegis timing effect is present between 10 and 20°C, that implies the following:

$R_{10,20}$ 1) increases when x increases from zero and 2) reaches a constant value with a sufficiently high x. This happens, at the latest, when the accumulated chilling x meets the chilling requirement of endodormancy release.

Correspondingly, if the Vegis timing effect is present between 20 and 30°C, that implies the following:

$R_{20,30}$ 1) increases when x increases from zero and 2) reaches a constant value with a sufficiently high x. This happens, at the latest, when the accumulated chilling x meets the chilling requirement of endodormancy release.

The rate of ontogenetic development for each forcing temperature, T_{forc}, and chilling duration, x, was first calculated with Eqn. (1). Subsequently, the values of the two ratios were calculated and plotted against the duration of chilling, x. With no Vegis timing effect assumed, an approximately constant horizontal line is predicted for both ratios, whereas the Vegis timing effect predicts that the value of one or both of the ratios increases with increasing duration of previous chilling, x (Fig. S2).

3. Results

3.1. *Occurrence of leaf-out*

The occurrence of leaf-out, measured by the budburst percentage, BB %, showed different responses to the three environmental cues examined in the different species (Fig. 2, Table 1). In *Phoebe*, all seedlings showed leaf-out, i.e., BB% was 100 % in all treatments (Fig. 2b). In *Castanopsis,* too, all seedlings reached the stage of leaf-out, but at the lowest forcing temperature 10°C the leaf-out was abnormal in part of the seedlings. This did not meet the criterion set for bud burst, so that the BB % values in the 10°C forcing remained somewhat below 100 % in *Castanopsis* (Fig. 2a). In *Pseudolarix* and *Torreya*, BB% showed a similar pattern, in broad terms, in 20 and 30°C forcing: BB% increased with increasing duration of chilling; and with short durations of chilling, BB% was higher in LD than in SD forcing, so that LD compensated for lack of chilling (Fig. 2c,d). For *Pseudolarix,* however, with forcing at 30°C, the pattern was not very clear because BB% was at or close to 100 % in both photoperiods and with all chilling durations (Fig. 2c).

In addition to *Castanopsis* (see preceding paragraph), *Pseudolarix* and *Torreya* also showed results in 10°C forcing that differed from those obtained at the two higher forcing temperatures. In *Pseudolarix*, BB% in 10°C forcing was 100 % for both photoperiods and all chilling durations (Fig. 2c). In *Torreya*, BB% in 10°C forcing fluctuated rather irregularly between about 25 and 75 % with different durations of chilling, but the compensating effect of LD with no or short duration of chilling was seen in *Torreya* even in 10°C forcing (Fig. 2d).

The BB% results obtained for *Pseudolarix* and *Torreya* evinced several significant interactions of the three environmental cues (Table 1). Because of the deviating results found for 10°C forcing, there was a strong interaction between forcing temperature and chilling duration in both species, and for *Pseudolarix* the interaction between forcing temperature and forcing photoperiod was also significant (Table 1). Because of the compensating effect of LD for lack of chilling, the interaction between chilling duration and forcing photoperiod was significant in *Torreya*. In *Pseudolarix*, the compensating effect was seen clearly in the 20°C forcing only (Fig. 2c), and for that reason the interaction of all three environmental cues was significant for *Torreya* (Table 1).

The Vegis occurrence effect predicts that after no or short chilling, the bud burst percentage, BB%, increases with increasing forcing temperature, but after prolonged chilling this temperature dependence of BB% disappears (Fig. S1a). This predicted pattern was not realized with any of the four species examined (Fig. 3). With *Phoebe*, no pattern of BB % was seen at all because BB% was 100 % in all treatments (Fig. 3b). With the exception of the abnormal bud burst in the 10°C forcing, BB% was also 100 % in all treatments with *Castanopsis* (Fig. 3a). For *Pseudolarix* and *Torreya*, various patterns for BB% were found (Fig. 3c,d), but they did not follow the one predicted by the Vegis occurrence effect (Fig. S1a). However, if the BB% value for 10°C forcing had been at or

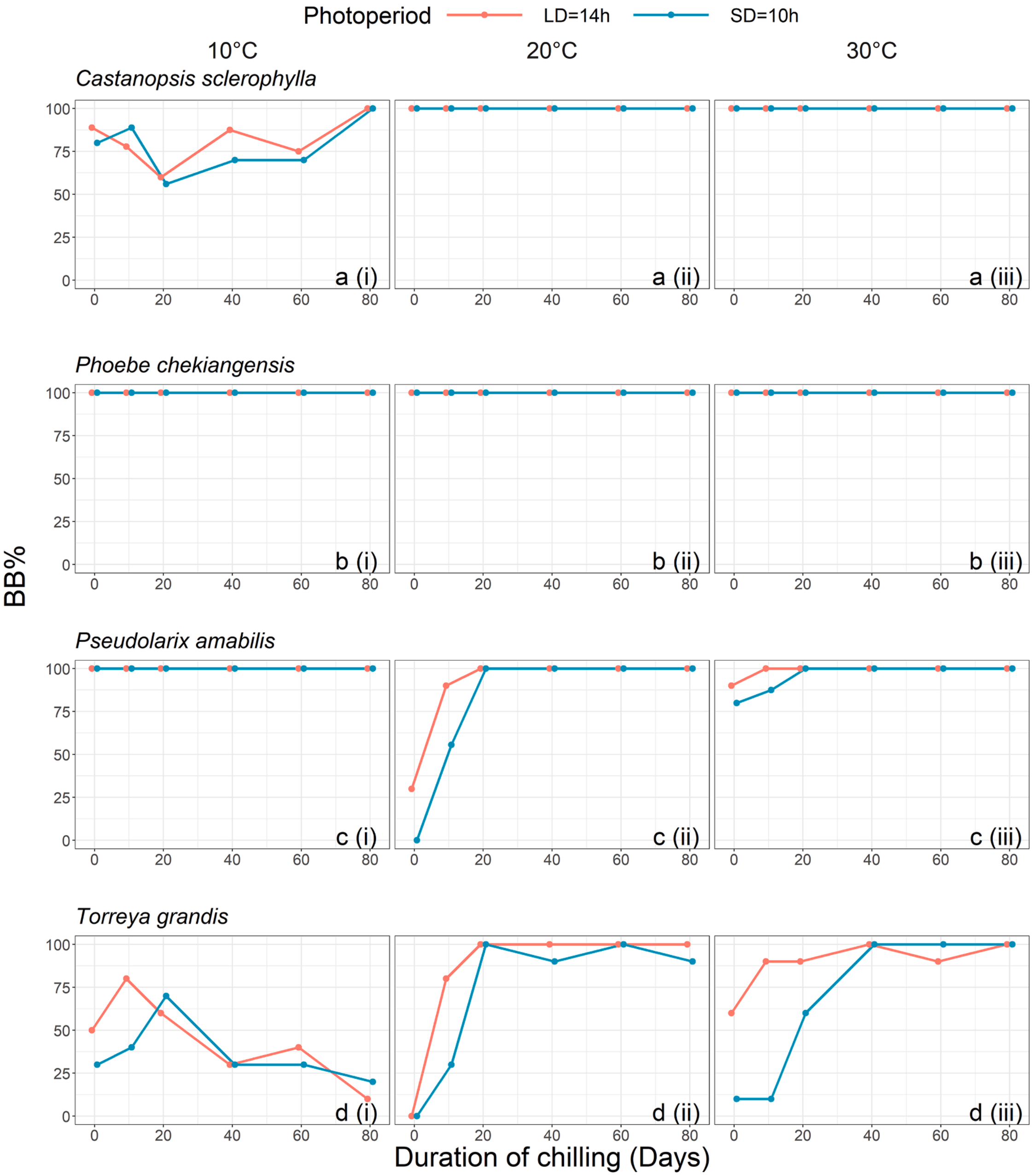

Fig. 2. Dependence of bud burst percentage, BB%, on the duration of chilling at +6°C (horizontal axes), the forcing air temperature (the three columns of the panels), and the forcing photoperiod (red lines = LD, blue lines = SD) in four subtropical tree species. The LD (14 h) and SD (10 h) forcing photoperiods were designed with reference to the natural seasonal variation of the day length at our subtropical study site. In the forcing conditions, the occurrence and the timing of bud burst was determined on the basis of leaf-out. (A) Seedlings of Castanopsis sclerophylla, (B) seedlings of Phoebe chekiangensis, (C) detached twigs of Pseudolarix amabilis, (D) seedlings of Torreya grandis. For details, see Fig. 1 and Material and methods.

near zero in the non-chilled *Pseudolarix* (0 days of chilling, Fig. 2ci), then the pattern predicted by the Vegis occurrence effect would have been approximately realized in that species (see Discussion for the possible explanation of that deviating data point).

3.2. *Timing of leaf-out*

The timing of leaf-out, as measured by days to bud burst, DBB, was affected significantly by the forcing temperature and chilling duration in all species and, for *Phoebe* and *Pseudolarix,* by the forcing photoperiod as well (Table 2, Fig. 4, S3). The forcing air temperature had the biggest quantitative effect in that DBB decreased by rising forcing temperatures (Fig. 4). The decrease was especially pronounced in the range of 10 to 20°C, whereas less dramatic reduction was seen in the range of 20 to 30°C. DBB also decreased with prolonged chilling, especially at the forcing temperature of 10°C (Fig. 4, S3). With short durations of chilling, the value of DBB was sometimes lower in LD than in SD, but the effect was not consistent and usually not very big. With *Pseudolarix,* however, forcing at 20°C was an exception as the DBB values with short durations of chilling were 10–45 days shorter under LD than under SD (Fig. 4c-ii).

Quite a few of the interactions between the environmental cues were also statistically significant. Most importantly, similar to the BB%, the interaction of forcing temperature with chilling duration was significant in all species (Table 2). This was seen in all species as flattening of the DBB curve in forcing temperatures of 10 to 30°C (Fig. 4).

The Vegis timing effect predicts that one or two of the ratios of the

Table 1

A logistic regression analysis with a binary response (bud burst / no bud burst) of the factors affecting the percentage of bud burst, BB%, in detached twigs of Pseudolarix amabilis and seedlings of Torreya grandis. No statistical analysis of BB% was carried out with seedlings of Castanopsis sclerophylla and Phoebe chekiangensis because in these two species the value of BB% was at or near 100 % in all treatments. 'Chilling' denotes the duration of the chilling treatment; and 'Photoperiod' the photoperiod (10 h, 14 h) and 'Temperature' the air temperature (+10, +20, +30°C) prevailing in the forcing conditions after the chilling treatment. Statistically significant P values <0.05 are indicated with a bold font.

		Pseudolarix	*Torreya*
Chilling	P	**<0.001**	**<0.001**
Photoperiod	P	0.132	**<0.001**
Temperature	P	**<0.001**	**<0.001**
Chilling * Photoperiod	P	0.151	0.159
Temperature * Photoperiod	P	0.027	0.047
Temperature * Chilling	P	**<0.001**	**<0.001**
Chilling* Photoperiod * Temperature	P	0.020	0.047

rates of development, calculated with the DBB values observed for the three forcing temperatures, increases when the duration of chilling, x, increases from zero and reaches a constant value with a sufficiently high value of x (Supporting Information method 1; Fig. S2). No such effect was found for *Castanopsis* or *Phoebe* (Fig. 5a,b). In *Pseudolarix,* a clear Vegis timing effect was found in the upper temperature range of 20 to 30°C in that depending on the photoperiod, $R_{20,30}$ rose from 0.3 – 0.4 at 10 days of chilling to 0.6 – 0.8 at 60 days of chilling (Fig. 5c). A less dramatic increase was found in *Torreya* for $R_{20,30}$ from 10 to 40 days (Fig. 5d). The patterns of the two ratios were similar in general for SD and LD, though there were differences in the exact values of the ratios between the two photoperiods. In *Torreya*, $R_{10,20}$ increased with 40 to 80 days of chilling (Fig. 5d), but this increase, observed with long durations of chilling only, is not the one predicted by the Vegis timing effect. In all, these results provide support for the existence of the Vegis timing effect in *Torreya* and *Pseudolarix* within the higher temperature range of 20 to 30°C but not within the lower temperature range of 10 to 20°C.

In some cases the values of one or both of the two ratios also decreased with increased duration of chilling because of random variation in the data. A clear case of this was seen in *Pseudolarix* $R_{10,20}$ under SD forcing after 10 – 20 days of chilling (Fig. 5c). The value of $R_{10,20}$ was exceptionally high after 10 days of chilling: $R_{10,20} = 0.958$ (Fig. 5c). This indicates that the rates of development under SD were almost equal in 10°C (Fig. 4ci) and 20°C (Fig. 4cii) forcing. The outlying observation obtained in 20°C forcing was probably caused by the low BB% = 50 % (Fig. 2cii), indicating that only 5 twigs showed leaf-out in that treatment.

4. Discussion

Our aim was to conduct a simultaneous study of the effects and interactions of the duration of chilling, forcing temperature, and forcing photoperiod on the occurrence and timing of leaf-out in four subtropical tree species. In particular, we examined the interaction of chilling duration and forcing temperature, which had been suggested by Vegis (1964) already but has received little attention since. In addition to the interaction originally suggested by Vegis (1964) for the occurrence of leaf-out, we also examined the corresponding interaction suggested by Lundell et al. (2020) for the timing of leaf-out. To facilitate the testing of the latter, we introduced a novel method. Our results show that all three

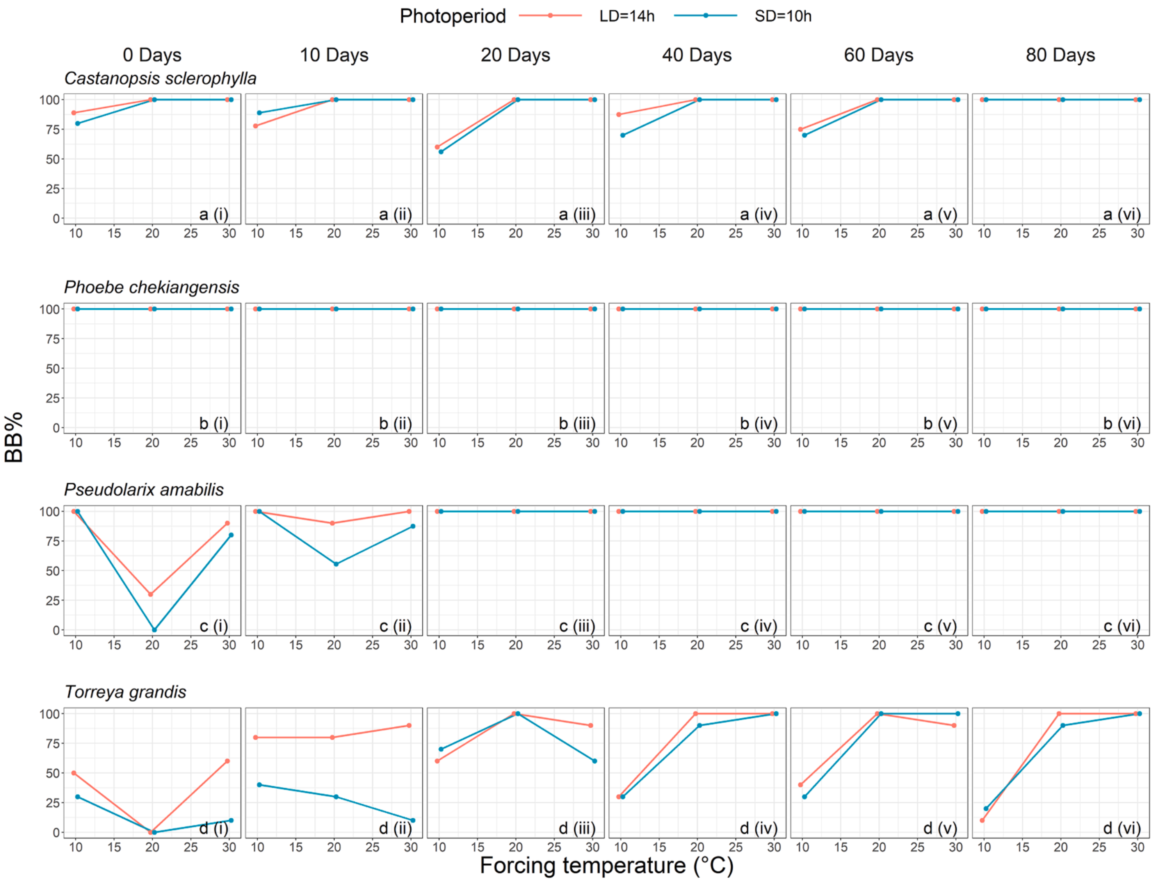

Fig. 3. Test of the Vegis occurrence effect with four subtropical tree species: the bud burst percentage, BB%, as a function of the forcing temperature after 0 – 80 days of chilling indicated by the six columns of the panels. (A) Seedlings of Castanopsis sclerophylla, (B) seedlings of Phoebe chekiangensis, (C) detached twigs of Pseudolarix amabilis, (D) seedlings of Torreya grandis. For the patterns predicted by the Vegis occurrence effect, see Materials and methods and Fig. S1.

Table 2
Analysis of variance of the factors affecting the days to bud burst, DBB, in seedlings of Castanopsis sclerophylla, Phoebe chekiangensis, and Torreya grandis and in detached twigs of Pseudolarix amabilis under the forcing conditions. ‘Chilling’ denotes the duration of the chilling treatment; and ‘Photoperiod’ the photoperiod (10 h, 14 h) and ‘Temperature’ the air temperature (+10, +20, +30°C) prevailing in the forcing conditions after the chilling treatment. Statistically significant P values <0.05 are indicated with a bold font.

		Castanopsis	*Phoebe*	*Pseudolarix*	*Torreya*
Chilling	F	118.668	172.884	280.531	33.043
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Photoperiod	F	0.02	15.664	69.721	0.569
	P	0.888	**<0.001**	**<0.001**	0.452
Temperature	F	3120.931	8743.044	1878.436	1034.428
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Chilling * Photoperiod	F	1.088	7.788	7.01	6.136
	P	0.367	**<0.001**	**<0.001**	**<0.001**
Temperature * Photoperiod	F	0.501	1.797	19.386	4.824
	P	0.607	0.168	**<0.001**	**0.009**
Temperature * Chilling	F	19.716	84.763	46.499	8.608
	P	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Chilling* Photoperiod * Temperature	F	1.246	3.467	4.583	5.927
	P	0.262	**<0.001**	**<0.001**	**<0.001**

environmental cues affected leaf-out both individually and interactively. However, there were considerable differences, both between the cues in the mode and the extent of their effects and between the four tree species in their responses to the cues. These results suggest that the responses of different subtropical tree species to climatic warming will be different.

4.1. Dominance of forcing temperature in castanopsis and phoebe

In our study the occurrence of leaf-out in *Castanopsis* and *Phoebe* was not dependent on chilling duration, as even unchilled seedlings showed leaf-out (Fig. 2a,b). In *Castanopsis,* leaf-out in part of the seedlings was abnormal in 10°C forcing, but this was probably because for *Castanopsis,* 10°C is close to the lower threshold temperature for ontogenetic development towards leaf-out (Zhang et al., 2022). On the basis of similar findings of BB% = 100 % with all durations of chilling, Zhang et al. (2021a) concluded that these two species have a relatively shallow endodormancy. As Zhang et al. (2021a) used only one forcing temperature and one forcing photoperiod in their study, the present study, with six different combinations of two photoperiods and three forcing temperatures, confirms the robustness of the conclusion of Zhang et al. (2021a). Despite some statistically significant effects and interactions of photoperiod, in quantitative terms the timing of leaf-out in *Castanopsis* and *Phoebe* was affected mainly by the forcing temperature and its interaction with chilling duration (Fig. 4). The interaction of these two cues, however, was not the of the kind predicted by the Vegis timing effect.

Overall, with the earlier findings of Zhang et al. (2021a), these results suggest that the leaf-out phenology of *Castanopsis* and *Phoebe* is dominated by the ecodormancy release, i.e., the microscopic ontogenetic development towards leaf-out in the buds rather than the endodormancy release, i.e., the removal of the growth-arresting environmental conditions inside the buds (Fuchigami et al., 1982; Lang et al., 1987). This is because leaf-out was observed in all treatments and its timing was affected mainly by the forcing temperature. Accordingly, the non-linear effect of the forcing temperature on the rate of ontogenetic development (Zhang et al., 2022) is crucial for the timing of leaf-out in *Castanopsis* and *Phoebe*.

4.2. Complex interactions of cues in pseudolarix and torreya

In *Pseudolarix*, all twigs, including unchilled ones, showed leaf-out when forced at 10°C but not when forced at 20°C (Fig. 2c). The leaf-out seen in 10°C forcing with unchilled twigs was most probably the result of the endodormancy-releasing effect of this low forcing temperature. This notion is supported by the findings of Zhang et al. (2022), who showed that 10°C causes endodormancy release in *Pseudolarix*. Hänninen (1990) found a similar phenomenon in boreal *Picea abies,* as unchilled seedlings showed bud burst when forced at 12°C but not when forced at 17 or 22°C.

Without the endormancy-releasing effect of the forcing temperature 10°C, the BB% value of the unchilled *Pseudolarix* twigs (0 weeks of chilling) could have been 0 %. If that value is assumed for BB% with 0 days of chilling (Fig. 3ci), then a pattern arises that is roughly similar to the one predicted by the Vegis occurrence effect. This reasoning suggests that the Vegis occurrence effect may occur in *Pseudolarix*, but this notion is far from being conclusive. On the contrary, a strong and long-lasting (20 to 60 days of chilling) Vegis timing effect was seen in *Pseudolarix* twigs in the temperature range of 20 to 30°C (Fig. 5c). Lastly, in *Pseudolarix,* LD was found to compensate for lack of chilling in both the occurrence (Fig. 2) and the timing (Fig. 4) of leaf-out.

In *Torreya* seedlings, BB% fluctuated irregularly in 10°C forcing (Fig. 2d). These deviating results probably came about because 10°C is close to the lower limit of the temperature range allowing ontogenetic development towards leaf-out in *Torreya* (Zhang et al., 2022). At the two higher forcing temperatures, results similar to those found by Zhang et al. (2021b) were obtained for the occurrence of leaf-out: BB% increased with increased duration of chilling, and LD compensated for insufficient chilling with short durations of chilling (Fig. 2d). No evidence for the Vegis occurrence effect was found for *Torreya* (Fig. 3d).

The results obtained for DBB in *Torreya* were in line with those found by Zhang et al. (2021b), who used only one forcing temperature in their study: DBB decreased with prolonged chilling and LD compensated for insufficient chilling (Fig. 4d). Furthermore, our results for *Torreya* provided evidence for the Vegis timing effect in the temperature range of 20 to 30°C (Fig. 5d), but the effect was not so strong and long-lasting as it was in Pseudolarix (Fig. 5d).

In all, contrary to the relatively simple results obtained for *Castanopsis* and *Phoebe*, quite complex interactions of the three environmental cues were found in the regulation of leaf-out in *Pseudolarix* and *Torreya*. In contrast to *Castanopsis* and *Phoebe*, not only the timing of leaf-out but also its occurrence was affected by the interactions of the environmental factors in *Pseudolarix* and *Torreya*. This suggests that the interactions were related not only to the ontogenetic development towards leaf-out the buds (Wang et al., 2020b) but also to the endodormancy release, i. e., the removal of growth-arresting conditions.

4.3. Implications for process-based modeling and the effects of climate change

The environmental regulation of the endodormancy release and the spring phenology of trees has been addressed in past few decades with process-based tree phenology models, which are widely used in assessing the ecological effects of climatic change (for reviews, see Hänninen, 2016; Chuine & Régnière 2017; Hänninen et al., 2019; Zhao et al., 2020). However, to the best of our knowledge, the interaction suggested by Vegis (1964) almost sixty years ago has only been addressed in the model developed by Lundell et al. (2020) for boreal field layer plants. For subtropical trees, process-based tree spring phenology models were published by Chen et al. (2017) and Zhang et al. (2022), and neither of the Vegis effects examined in the present study was addressed in those studies. Our limited yet novel results suggest that one or both of the Vegis effects appear in some, but not in all, subtropical tree species, so that the effects need to be addressed in further experimental studies aiming at developing realistic process-based tree phenology models for subtropical trees. Furthermore, as the Vegis effect has been shown to affect the trees’ response to climatic warming (Hänninen, 2016), our species-specific results suggest that the different subtropical tree species respond to climatic warming differently.

Lundell et al. (2020) found experimental evidence for the Vegis

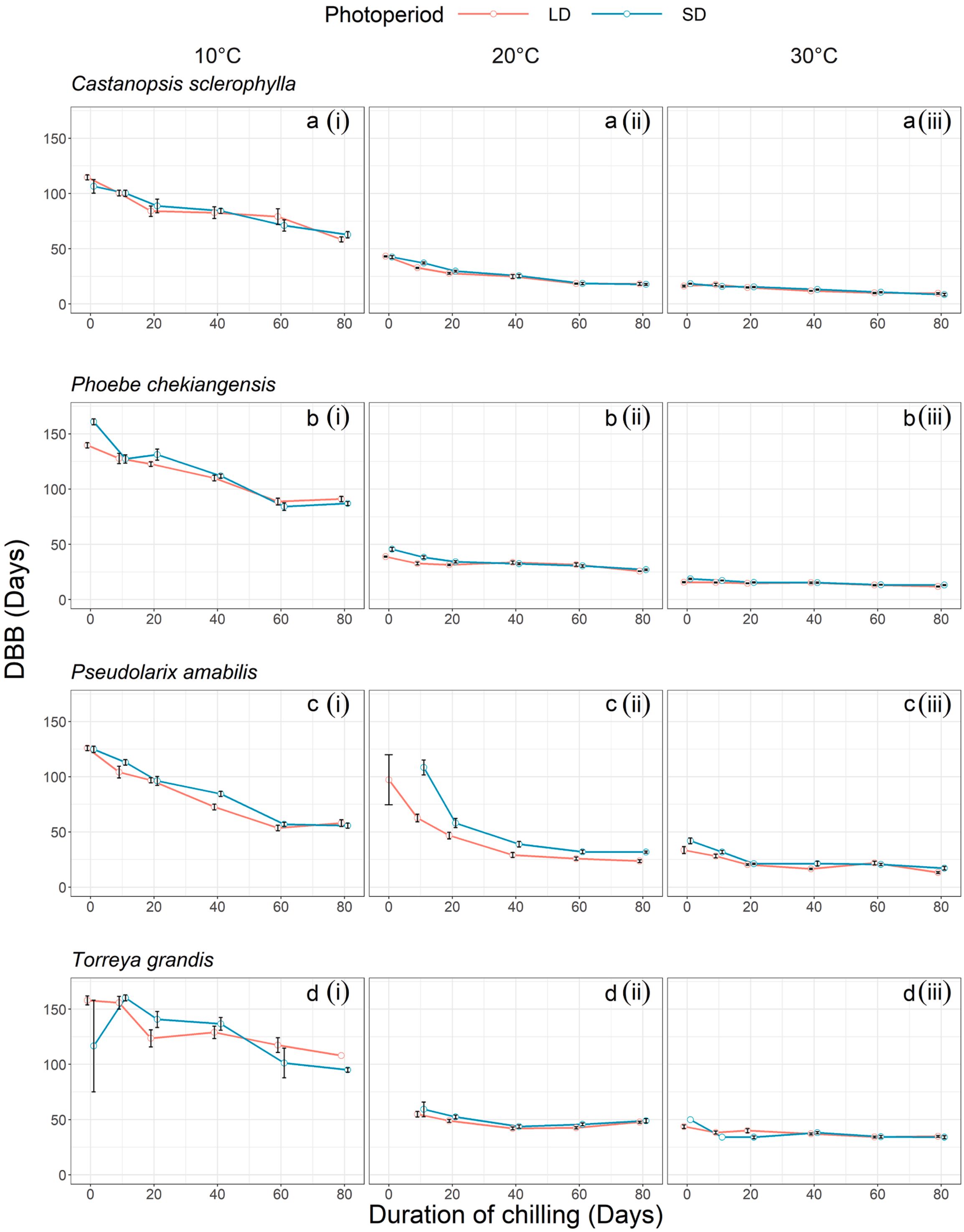

Fig. 4. Dependence of days to bud burst, DBB (mean ± SE), on the duration of chilling at +6°C (horizontal axes), the forcing air temperature (the three columns of the panels), and the forcing photoperiod (red lines = LD, blue lines = SD) in four subtropical tree species. The LD (14 h) and SD (10 h) forcing photoperiods were designed with reference to the natural seasonal variation of the day length at our subtropical study site. In the forcing conditions, the occurrence and the timing of bud burst was determined on the basis of leaf-out. (A) Seedlings of Castanopsis sclerophylla, (B) seedlings of Phoebe chekiangensis, (C) detached twigs of Pseudolarix amabilis, (D) seedlings of Torreya grandis. For details, see Fig. 1 and Material and methods. The case where data point was missing indicated none of seedlings had bud burst.

theory for some, but not for all, of the boreal field layer plant species they examined. Now we found a similar result for subtropical tree species. Considered together, these results highlight the need to develop species-specific process-based tree phenology models. In real trees the responses to environmental cues vary between species, so that any research strategy aiming at a generalized 'consensus model' for all species would not be successful.

The process-based tree phenology models developed for subtropical trees (Chen et al., 2017; Zhang et al., 2022) do not address the effects of photoperiod. For *Castanopsis* we did not find any effects of photoperiod,

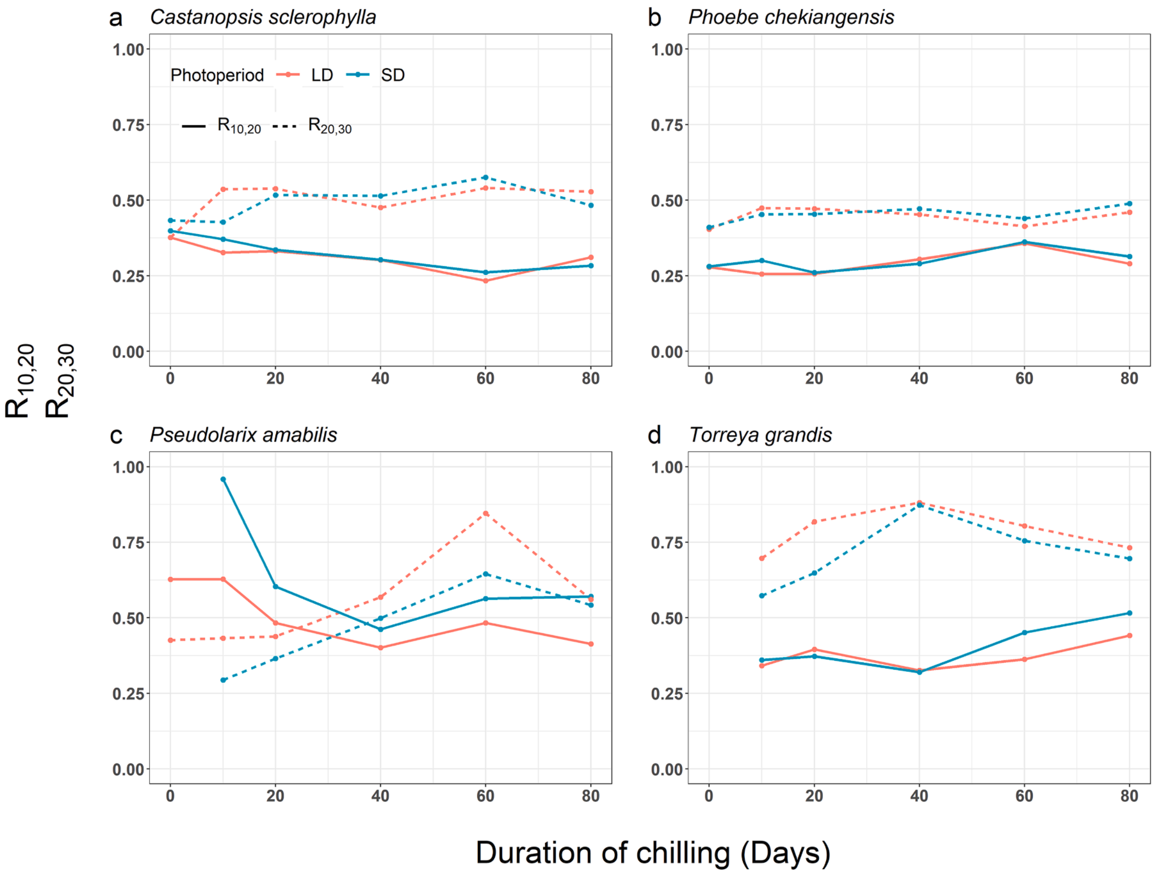

Fig. 5. Test of the Vegis timing effect with four subtropical tree species: the values of the ratios R10,20 (continuous lines) and R20,30 (dashed lines) as a function of the duration of the previous chilling. The results are shown separately for LD (red symbols) and SD (blue symbols). (A) Seedlings of Castanopsis sclerophylla, (B) seedlings of Phoebe chekiangensis, (C) detached twigs of Pseudolarix amabilis, (D) seedlings of Torreya grandis. For the patterns predicted by the Vegis timing effect, see Materials and methods, Supporting information method 1, and Fig. S1.

but for the other tree species examined, our results implied a need to include photoperiod in the model development. This need remains to be evaluated in further modeling studies. This is because due to the principle of parsimony, relatively small yet statistically significant effects may be neglected in modeling studies, where simplifications are always needed. Even so, in the subtropical *Liriodendron chinense,* photoperiod has been found to regulate the occurrence of leaf-out (Zhang et al., 2021b), so that for that subtropical tree species at least, photoperiod needs to be included in the development of process-based phenology models. The effects of photoperiod have been included in some previous models developed for boreal and temperate trees (Caffarra et al., 2011; Vitasse and Basler, 2013; Meng et al., 2021), so that they may be used as a starting point when the effect of photoperiod is introduced into process-based models developed for subtropical tree species.

5. Conclusion

This study provides first-time multifactorial experimental evidence for the effects and interactions of three environmental cues, i.e., chilling duration, forcing temperature, and forcing photoperiod, in regulating leaf-out in subtropical trees. In particular, we addressed the specific interaction that was introduced almost sixty years ago (‘Vegis effect’; Vegis, 1964) but has been largely forgotten since. We introduced a method for testing the Vegis effect against experimental results. The environmental cues were found to display several effects and interactions. Most importantly, our results show big differences among the four sympatric tree species growing in our subtropical study site in regard to their responses to the environmental cues. For instance, *Pseudolarix amabilis* and *Torreya grandis* showed evidence for the Vegis effect but *Castanopsis sclerophylla* and *Phoebe chekiangensis* did not. These species-specific findings show the importance of well-designed multi-factorial experiments for developing process-based phenology models for subtropical and other extratropical tree species. Lastly, the species-specific findings also suggest that different subtropical trees respond quite differently to climatic warming, but the particular differences between species remain to be tested in forthcoming studies.

Conflict of interest

Authors claim no conflicts of interest.

Author contributions

RZ, JW and HH planned and designed the experiment. LZ conducted the experiment. LZ, RZ, JZ and HH analyzed the data and drafted the manuscript with input from RB and JW. All authors contributed to the article and approved the submitted version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

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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.2022.109227.

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