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Beyond rest and quiescence (endodormancy and ecodormancy): A novel model for quantifying plant–environment interaction in bud dormancy release

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Abstract

Bud dormancy of plants has traditionally been explained either by physiological growth arresting conditions in the bud or by unfavourable environmental conditions, such as non-growth-promoting low air temperatures. This conceptual dichotomy has provided the framework also for developing process-based plant phenology models. Here, we propose a novel model that in addition to covering the classical dichotomy as a special case also allows the quantification of an interaction of physiological and environmental factors. According to this plant–environment interaction suggested conceptually decades ago, rather than being unambiguous, the concept of "non-growth-promoting low air temperature" depends on the dormancy status of the plant. We parameterized the model with experimental results of growth onset for seven boreal plant species and found that based on the strength of the interaction, the species can be classified into three dormancy types, only one of which represents the traditional dichotomy. We also tested the model with four species in an independent experiment. Our study suggests that interaction of environmental and physiological factors may be involved in many such phenomena that have until now been considered simply as plant traits without any considerations of effects of the environmental factors.

KEYWORDS

chilling, dormancy, ecodormancy, endodormancy, forcing, growth onset, phenology models, post-rest, quiescence, rest

1 | INTRODUCTION

Most perennial northern plants cease growth and enter a state of bud dormancy at the onset of winter, with a concomitant increase in frost hardiness. During spring, an opposite sequence of developmental phenomena leading to a loss of frost hardiness and growth onset takes place. At the whole plant level, this annual cycle of growth and dormancy is relatively well understood in trees and other woody plants (Fuchigami, Weiser, Kobayashi, Timmis, & Gusta, 1982; Hänninen, 2016; Hänninen & Tanino, 2011; Sarvas, 1972, 1974), whereas much less is known about the annual cycle of herbaceous northern perennials (Yoshie & Yoshida, 1989). Furthermore, despite the progress during the last few decades, the molecular and physiological mechanisms of the annual cycle remain still only partially understood in woody plants (Arora, Rowland, & Tanino, 2003; Brunner, Evans, Hsu, & Sheng, 2014; Cooke, Eriksson, & Junttila, 2012; Fan et al., 2010; Horvath, Anderson, Chao, & Foley, 2003; Junttila, 2007; Kudoh, 2016; Lee et al., 2017; Rinne & van der Schoot, 2003; Rohde & Bhalerao, 2007; Tanino, Kalcsits, Silim, Kendall, & Gray, 2010; Tylewicz et al., 2018; Zhang et al., 2018). So, as molecular markers are not yet available for quantifying the dormancy status of the bud, studies on rest break need still to be based on observations of growth

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onset in chilling–forcing experiments carried out at the whole plant level (Hänninen et al., 2019).

Bud dormancy of plants has traditionally been explained either by physiological growth arresting conditions in the bud or by unfavourable environmental conditions, such as non-growth-promoting low air temperatures. According to the terminology adopted in the present study (Fuchigami et al., 1982; Hänninen, 2016; Hänninen et al., 2019; Hänninen & Kramer, 2007; Weiser, 1970), the former is referred to as rest (endodormancy in the terminology of Lang, Early, Martin, & Darnell, 1987), and the latter as quiescence (ecodormancy in the terminology of Lang et al., 1987). During the last decades, this traditional conceptual dichotomy has been also the basis for developing process-based simulation models for boreal and temperate trees (for reviews, see Chuine, de Cortazar-Atauri, Kramer, & Hänninen, 2013; Chuine & Régnière, 2017; Hänninen, 2016; Hänninen & Kramer, 2007). In addition to trees, these models have also been applied to dwarf shrubs (Pop, Oberbauer, & Starr, 2000; Van Wijk, Williams, Laundre, & Shaver, 2003) and herbaceous crop cultivars (Tanino & Wang, 2008), but as far as we know, not to native herbaceous plants. Currently, these models are often used for assessing the effects of climatic warming on the springtime phenology of trees (Chen, Wang, & Inouye, 2017; Chuine et al., 2016; Hänninen, 2016).

In process-based plant phenology models, effects of environmental factors, mainly air temperature, on two processes are quantified (see Chuine et al., 2013 and Hänninen, 2016, and the references therein): First, exposure to low chilling temperatures drives the process of rest break, that is, the removal of the growth arresting physiological conditions in the buds (chilling requirement of rest completion). Second, exposure to high forcing temperatures drives the process of ontogenetic development, that is, the microscopic anatomic changes in the bud leading to visible bud burst (high temperature requirement of growth onset). The state of rest break affects the rate of ontogenetic development in the models, but following the conceptual dichotomy of rest and quiescence, there is no interaction between the state of rest break and the prevailing air temperature. In other words, the form of the air temperature response of rate of ontogenetic development is similar in different phases of the rest period, even though the level of the curve varies (Figure 1a).

The conceptual dichotomy of rest and quiescence was originally questioned by Vegis (1964) who presented for the dormancy phenomena of higher plants an alternative conceptual model based on interaction of the rest status and prevailing air temperature. According to Vegis' (1964) conceptual model, the growth promoting temperature range gets narrower as rest is induced during a period referred to as pre-rest and gradually widens again as rest is broken during a period of post-rest. Some plants exhibit a period of true rest between pre- and post-rest, in which growth does not occur at any temperature. Vegis (1964) introduced various types of the narrowing (pre-rest) and widening (post-rest) of the growth promoting temperature range. Accordingly, in northern plants, growth is possible during pre- and post-rest in relatively high, but not in low, temperatures. This phenomenon is well documented in dormant seeds of many northern plants that have been observed to germinate during dormancy in high but not in low temperatures (Junttila, 1970, 1976; Salažs & Ievinsh, 2004). Junttila and

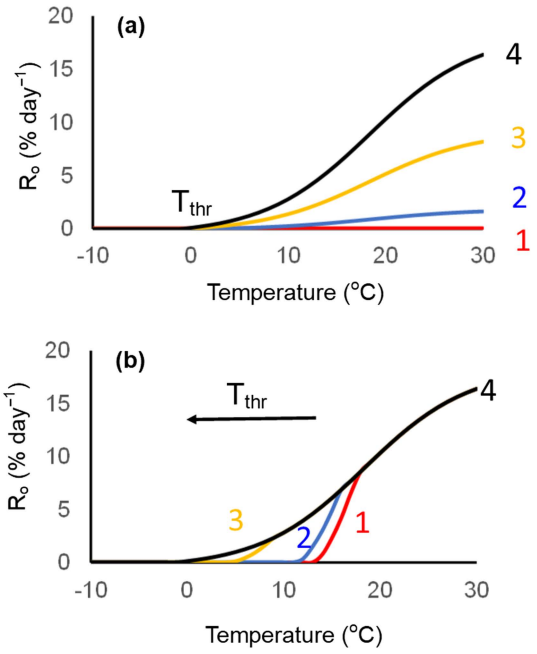

FIGURE 1 Two models of bud dormancy release and growth onset in plants (Hänninen et al., 2019). In both figures, R_o denotes the rate of ontogenetic development towards growth onset. (a) The classical model based on a dichotomy of rest (endodormancy) and quiescence (ecodormancy). During quiescence, development is arrested only in low temperatures below the threshold of the growth-promoting temperature range, T_{thr}, above the threshold development occurs at the maximal rate allowed by the prevailing temperature (black curve 4). At the beginning of rest, the development is arrested in all temperatures (red curve 1). As a result of rest break caused by chilling, the ontogenetic competence in temperatures above the threshold T_{thr} is gradually increased (blue curve 2 and orange curve 3) until chilling requirement of rest completion is met and quiescence is attained (black curve 4). (b) The novel model based on the interaction of state of rest break and prevailing air temperature. The threshold T_{thr} is not constant but shifts to lower temperatures as a result of chilling. The form of the response curve also changes during rest break. The curves with different colors and numbers indicate similar phases as in (a)

Hänninen (2012) found support for Vegis's (1964) conceptual model also with buds of *Betula pendula* and *Betula pubescens* seedlings. However, compared with the widely used conceptual model based on the dichotomy of rest and quiescence, Vegis's (1964) conceptual model including the interaction has been only rarely addressed with buds of northern plants (Cooke et al., 2012; Hänninen, 1990). Furthermore, Vegis' (1964) conceptual model has not been addressed in quantitative terms as it has not been included in process-based tree phenology models (but see Section 4). This is unfortunate, because when revisiting Vegis' (1964) conceptual model, Hänninen (2016) found that the model has a high potential for improving our understanding of dormancy phenomena in northern perennial plants.

Here, we introduce a novel model for the quantification of plant–environment interaction in bud dormancy release (Figure 1b). The model

is flexible such that the extent of the interaction can vary depending on the particular experimental results obtained for the examined plant species. The model includes as a special case the classical model based on the dichotomy of rest and quiescence with no interaction of state of rest break and prevailing air temperature (Figure 1a). We parameterize the model for seven boreal field layer plant species with results from a growth chamber experiment where the timing of growth onset of the plants is observed in particular temperature treatments designed for estimating the model parameter values. No molecular or physiological markers are available for observing directly the quantitative progress of rest break (Hänninen et al., 2019), so our modelling is based on the hypothetico-deductive approach where the rest break processes are examined indirectly based on their implications to the timing of growth onset at the whole plant level (Hänninen, 2016). On the basis of the estimated parameter values, we make inferences about the chilling requirement of rest completion and the extent of the interactive effect in each of the examined seven plant species. Finally, we carry out an independent test of the model by data from an experiment where growth onset of the plants was observed in growth chambers after the plants had overwintered in different climatic conditions in the field at different geographical locations.

2 | MATERIAL AND METHODS

2.1 | Growth onset experiment

Plants of seven boreal field layer species common in Finland were grown in pots from either seeds or from plants planted in the pots after collecting them from their natural growing site. The species were chosen to represent various growth forms from either a boreal forest floor or a meadow habitat (Table 1). The seeds were sown and the plants planted in early spring 2008, and the plants were grown in pots outdoors over the summer and autumn at the Viikki Campus of the University of Helsinki, Finland (60°13.6′N, 25°1.2′E). In the autumn, the height of the plants varied between 1 and 2 cm (*Fragaria vesca* and *Hypericum perforatum*) and 10 and 15 cm (*Vaccinium myrtillus* and *Vaccinium vitis-idaea*). On October 15, 2008, the potted plants were gently packed in cardboard boxes and transported to a dark freezer storage room at the Finnish Forest Research Institute (currently the Natural Resources Institute Finland) research station in central Finland in Suonenjoki, where they were kept at a constant temperature of −2.5°C.

On four occasions during the winter (November 11, 2008, December 30, 2008, February 10, 2009, and March 17, 2009), a subset of the plants was transported back to the Viikki Campus and transferred to four growth chambers (Sanyo ML-350) at +5°C, +10°C, +15°C, and +20°C, respectively, with 10 plants per species in each treatment (eight plants for *Oxalis acetosella*). In all temperature treatments, the day length in the chambers for the four transfers was 8, 6, 8, and 10.5 hr, respectively, which approximated the natural day length outdoors at the time of the transfer. The light intensity in the chambers was moderately low. The plants were monitored every day, and the date of growth onset was determined following rules designed separately for each species according to the phenomena typical for its growth onset (Table 1). Subsequently, the number of days required for growth onset after the transfer to the growth chamber was counted.

TABLE 1 The growth forms, typical habitats, and the growth onset criteria of the species studied

Species	Growth form	Habitat	Growth onset criterion
Fragaria vesca	Rosette plant, winter leaves overwintering	Meadows	New leaf pushing out from "bud" cover (stipules)
Hypericum perforatum	Rhizomatous herb	Meadows	New leaves forming at the shoot apex
Leucanthemum vulgare	Overwintering rosette	Meadows	New leaves emerging
Linnaea borealis	Dwarf shrub with prostrate (creeping) stems and overwintering leaves	Boreal forest floor	New leaves emerging from bud
Oxalis acetosella	Rhizomatous herb with overwintering leaves	Boreal forest floor	New leaves emerging
Vaccinium myrtillus	Deciduous dwarf shrub	Boreal forest floor	Green leaf visible in breaking bud
Vaccinium vitis-idaea	Dwarf shrub, wintergreen leaves	Boreal forest floor	Bud opening

2.2 | A model for rest break and growth onset

In the current process-based phenological models, the state of rest break is in general simulated by accumulating chilling temperatures and the state of ontogenetic development by accumulating high (forcing) temperatures (Chuine et al., 2013; Chuine & Régnière, 2017; Hänninen, 2016; Hänninen & Kramer, 2007). The accumulation of the chilling regulates the high temperature accumulation, thus simulating the real-world phenomenon where the rest condition regulates rate of ontogenetic development towards bud burst. Among the different formulations used for describing this phenomenon in the tree phenology models, the one based on the concept and variable of *ontogenetic competence* (Hänninen, 1990, 2016; Hänninen & Kramer, 2007) was applied in the present study. The ontogenetic competence, C_o, is a dimensionless [0, 1] multiplier mediating the effect of rest status on the rate of ontogenetic development. When ontogenetic development is fully arrested during rest, the bud has no ontogenetic competence (C_o = 0). Ontogenetic competence is restored from C_o = 0 to C_o = 1 during rest break, either abruptly as in sequential models (Richardson, Seeley, & Walker, 1974; Sarvas, 1972, 1974), or gradually, as in parallel models (Figure 1a; Campbell, 1978; Campbell & Sugano, 1975; Cannell & Smith, 1983; Landsberg, 1974).

As the starting point of our novel model, we use the parallel model, as formulated by Hänninen (1990, 2016) and Hänninen and Kramer (2007). That formulation is structured by means of three submodels (Figure 2): one for the progress of rest break, one for the progress of ontogenetic development, and one for the ontogenetic competence. The submodel for the ontogenetic competence ties the two other submodels together. In the parallel model, the value of the ontogenetic competence is determined by the state of rest break, whereas in the novel model developed in the present study, it is determined by an interaction of the state of rest break and the prevailing temperature (Figure 2).

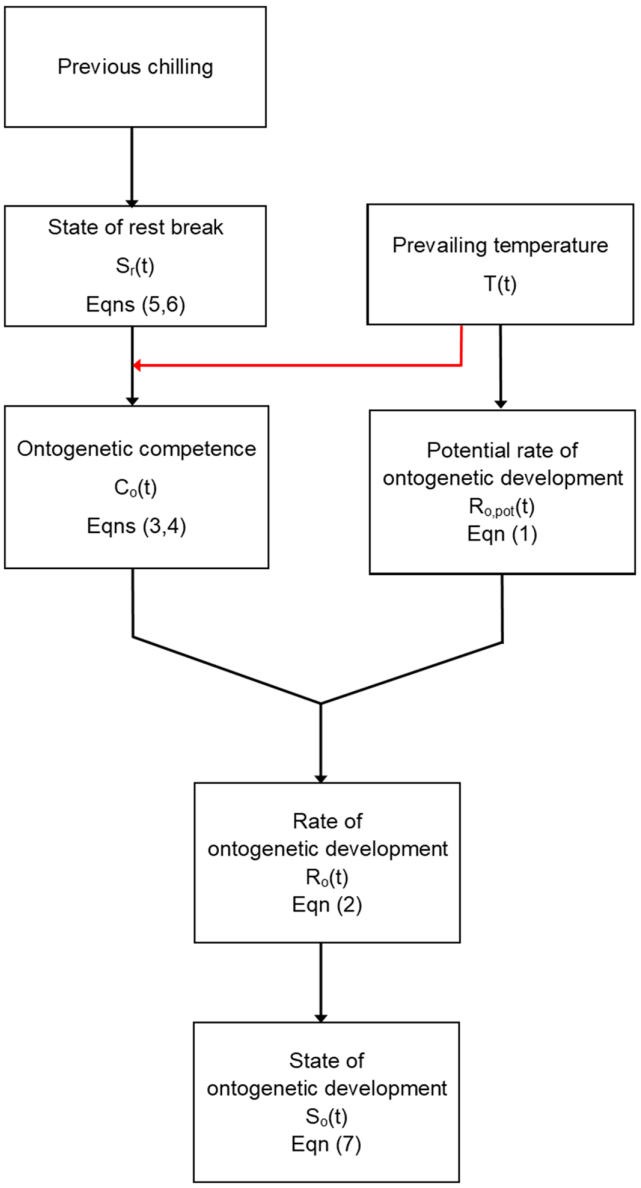

FIGURE 2 Principle of the rest break and growth onset model developed in the present study by introducing the interaction of state of rest break and prevailing air temperature (red arrow) into the parallel model (black boxes, lines, and arrows), the latter as formulated by Hänninen (1990, 2016) and Hänninen and Kramer (2007). In the parallel model, the ontogenetic competence is determined by previous chilling alone, whereas the novel model allows also the option of determining the ontogenetic competence by an interaction of state of rest break and prevailing temperature

The effect of temperature on the rate of ontogenetic development towards growth onset of plants with a fully satisfied chilling requirement, that is, the potential rate of ontogenetic development with respect to temperature, is given by the sigmoid temperature response curve (Figure 1a, black curve 4):

$$R_{o,pot}(t) = \begin{cases} 0 & T(t) < T_{thr} \\ \left(\frac{100}{H_{crit}}\right)\left(\frac{1}{1+\exp(-a(T(t)-b))}\right) & T(t) \geq T_{thr} \end{cases} \quad (1)$$

where $R_{o,pot}(t)$ is the potential rate of ontogenetic development at time t, $T(t)$ is the temperature, H_{crit} is the high temperature requirement of growth onset, T_{thr} is the low threshold temperature for ontogenetic development (Figure 1a), a is a parameter defining the steepness of the curve, and b is a parameter indicating the temperature at the inflexion point of the response curve (Hänninen, 1990, 2016; Hänninen & Kramer, 2007; Sarvas, 1972). Parameters a and b determine the shape of the sigmoid curve, whereas the reciprocal of the parameter H_{crit} is a scaling factor: The higher the value of H_{crit}, the lower is the potential rate of ontogenetic development at any given temperature T (see Hänninen, 2016, p. 64).

At time t, the actual rate of ontogenetic development $R_o(t)$ is given by Hänninen (1990, 2016) and Hänninen and Kramer (2007):

$$R_o(t) = C_o(t) \times R_{o,pot}(t), \quad (2)$$

where $C_o(t)$ is the ontogenetic competence, that is, a [0, 1] multiplier determining how large part of the potential rate of ontogenetic development is realized in the actual rate. In the parallel model, the value of $C_o(t)$ increases from zero (or a minimal value) to unity when the accumulated chilling increases from zero to the critical amount required for rest completion. Subsequently, the sigmoidal air temperature response of rate of ontogenetic development is scaled up as a result of chilling accumulation (Figure 1a; Hänninen, 1990; Hänninen, 2016, p. 84; Hänninen & Kramer, 2007).

In the present study, the simple formulation of the parallel model for $C_o(t)$ was replaced by a novel formulation allowing also the interactive effect of state of rest break and prevailing temperature on $C_o(t)$ (Figures 1b and 2):

$$C_{o,prel}(t) = cT(t) - d + \frac{S_r(t)}{100}(d+1), \quad (3)$$

$$C_o(t) = \begin{cases} 0 & C_{o,prel}(t) < 0 \\ C_{o,prel}(t) & 0 \leq C_{o,prel}(t) \leq 1 \\ 0 & C_{o,prel}(t) > 1 \end{cases} \quad (4)$$

where $T(t)$ is temperature, $S_r(t)$ is the state of rest break at time t (see below), $C_{o,prel}(t)$ is an auxiliary variable needed for keeping the values of the ontogenetic competence, $C_o(t)$, in the range [0, 1], and c and d are parameters. This formulation accounts both for the period of true rest, that is, no ontogenetic development at any temperatures,

and the post-rest period, where the plant experiences ontogenetic development towards growth onset at high temperatures but not at low temperatures. When the value of both parameters c and d are zero, then the model reduces to the parallel model, so that the growth competence $C_o(t)$ does not depend on temperature.

The air temperature response of the rate of rest break was modelled as

$$R_r(t) = \begin{cases} 0 & T(t) < T_1 \\ \left(\frac{100}{C_{crit}}\right) & T_1 \le T(t) \le T_2 \\ 0 & T(t) > T_2 \end{cases} \quad (5)$$

where $R_r(t)$ is the rate of rest break at time t, C_{crit} is the chilling requirement for rest completion, and T_1 and T_2 are the upper and lower thresholds for the rest breaking temperature range, respectively. In order to approximate the real, probably more complicated temperature response of the rate of rest break (Hänninen, 2016; Hänninen et al., 2019; Hänninen & Kramer, 2007; Harrington, Gould, & StClair, 2010; Sarvas, 1974), a simple uniform temperature response was used because our chilling experiment only included one chilling temperature and thus did not allow the determination of the real temperature response of rest break.

The state of rest break at time t is then given by

$$S_r(t) = \sum_{i=t_0}^{t} R_r(i) \quad (6)$$

evaluated with a discrete time step of 1 day starting from t_0. The chilling requirement is met, and rest is completed when $S_r(t)$ reaches or exceeds 100, but as the state of ontogenetic competence starts increasing already before this, ontogenetic development towards growth onset is possible in the plant before rest is completed.

Growth onset occurs when the state of ontogenetic development, S_o, given by

$$S_o(t) = \sum_{i=t_0}^{t} R_o(i) \quad (7)$$

evaluated with a discrete time step of 1 day, reaches or exceeds 100 (Hänninen, 2016; Hänninen & Kramer, 2007).

2.3 | Estimation of model parameters

The results from the growth onset experiment were used to parameterize the rest break and growth onset model (Equations (1)–(7)). It was assumed that the chilling requirement was met, and rest was completed on March 17, 2009, when the last subset of plants was transferred from the freezer storage to the growth chambers. Accordingly, the experimental results of this transfer were taken as representative of the potential rate of ontogenetic development towards growth onset, $R_{o,pot}$, addressed in Equation (1), so that for each species, the values of the parameters H_{crit}, a, and b were determined by fitting Equation (1) to the results of that transfer. In order to determine the empirical value of $R_{o,pot}$ for each species and temperature (+5°C, +10°C, +15°C, and +20°C), the number of days required for growth onset after the transfer to the growth chamber by each individual plant at that particular temperature was first determined. Subsequently, the empirical value of $R_{o,pot}$ was calculated by multiplying by 100 the reciprocal of the average number of days required for growth onset (Campbell, 1978; Hänninen, 2016, p. 54; Sarvas, 1972). Finally, Equation (1) was fitted to the four empirical data points of $R_{o,pot}$ thus obtained.

The values of the parameters C_{crit}, c, and d were then determined for each seven species by running the full model (Equations (1)–(7)) starting from the day the plants were taken to the freezer storage, that is, t_0 = October 15, 2008. The parameter values that minimized the root-mean-square error between the modelled and the observed growth onset dates of the plants in all four temperatures at all four starting times of the growth chamber experiments were determined by using a simulated annealing optimization algorithm (Bertsimas & Tsitsiklis, 1993; Chuine, Cour, & Rousseau, 1998; Kirkpatrick, Gelatt, & Vecchi, 1983) with a slow, exponential annealing schedule (Nourani & Andresen, 1998). When running the model for estimating the three parameters (C_{crit}, c, and d), fixed values of the following parameters were used: In Equation (1), fixed species-specific estimated values of the parameters H_{crit}, a, and b were used (see above), and the value of T_{thr} was set at 0°C (Hänninen, 1990, 2016; Hänninen & Kramer, 2007). In Equation (4), the lower threshold temperature for chilling, T_1, was set at −3.4°C, which is the lowest effective chilling temperature according to Sarvas (1974); and the upper threshold temperature for chilling, T_2, was arbitrarily set at +4.4°C. This was based on a scrutinization of the experimental results and preliminary test runs with the model that showed that there was no indication of additional chilling taking place at the lower growth chamber temperatures (+5°C and +10°C) even in the two earliest plant transfer sets with limited previous chilling in the freezer storage. In other words, if a temperature higher than +4.4°C would have had a chilling effect, then in the early transfers, the time required to growth onset in the +5°C forcing (and to some extent also in the +10°C forcing) would have been shorter than without assuming any such chilling effect of the forcing temperature. The effect would have been more prominent at +5°C than at +10°C, but no such shortening was found in the preliminary model runs. The optimization algorithm was restarted from intermediate optima several times, and multiple runs were carried out to ensure the quality of the parameter values found. All simulations and optimizations were carried out with Wolfram Mathematica 8.04 (Wolfram Research, Illinois, USA).

2.4 | Independent model testing

The rest break and growth onset models parameterized with the growth chamber experiment were tested with data from an independent experiment with potted individual plants of *H. perforatum*, *F. vesca*, *V. vitis-idaea*, and *V. myrtillus*. The plants, grown outdoors at the Viikki Campus of the University of Helsinki, were divided in three groups of thirty potted plants per species and transferred on October 25 and 26, 2011, to overwintering sites at Nåtö biological station in the Åland

archipelago (60°2.8′N, 19°58.5′E), at Lammi biological station (Lammi, Hämeenlinna, 61°3.3′N, 25°2.6′E), and at the Viikki Campus. At each site, the potted plants were located on the ground in baskets (Figure S1), so that during winter, they were covered by snow, if any. The overwintering sites represent three different types of winter climate, but have approximately similar photoperiods, thus facilitating the independent testing of the model developed in the present study. The climate at Nåtö is slightly maritime with mild winters and an ephemeral snow cover, whereas the climate at Lammi is more continental with cold winters and a persistent snow cover. The climate at Viikki is intermediate between the two other sites. Subsets of 10 plants per species were brought back on three occasions from each of the overwintering sites and placed in growth chambers (Sanyo ML-350) at +10°C with a day length corresponding to the natural day length at the respective times of transfer (6, 8, and 13.5 hr, respectively). The transfers took place on December 14–15, 2011, January 21–22, 2012, and April 3–6, 2012. The plants were monitored daily, and the time of growth onset was determined as described above (Table 1).

For each of the four species, an independent model prediction for the timing of growth onset in the growth chamber was calculated. To this end, the model was run with its fixed species-specific parameter values estimated based on the results of the growth chamber experiment documented above, starting from the t_0 = October 15, 2011, using as input daily averages of hourly air temperature data gathered at each of the three overwintering sites using iButton temperature loggers positioned next to the pots about 10 cm above the ground and shielded with cylindrical PVC radiation shields. The temperature data were extended with growth chamber temperature data for the period following the transfer to the growth chambers. The results of the model simulations were compared with the independent observations of growth onset recorded in the growth chambers.

2.5 | Statistical analyses

The effects of the time of transfer to the growth chamber (November, December, February, and March) and the air temperature in the growth chamber (+5°C, +10°C, +15°C, and +20°C) on the number of days to growth onset was analysed by means of a two-way ANOVA, using SPSS software (version 16.0, SPSS Inc., Chicago, USA).

3 | RESULTS

With the exception of a few outliers, the growth onset percentage was at or near 100% in all treatments in *H. perforatum*, *Leucanthemum vulgare*, *Linnaea borealis*, and *O. acetosella* (Table S1). In *F. vesca* and *V. myrtillus*, no growth onset took place at +5°C in the November transfer, and in *V. myrtillus*, growth onset percentage in that transfer was well below 100% also at the higher temperatures between +10°C and +20°C. In *V. vitis-idaea*, the growth onset percentage at +5°C was low in the November and December transfers (Table S1).

As expected, growth onset required significantly fewer days at high than at low temperatures in all species in the growth chamber experiment (Figure 3, $P < .001$; Table 2). However, there were differences among species in how this temperature response changed over the course of the experiment according to the transfer time. In *H. perforatum*, there was practically no difference in the response among transfer times so that at each temperature, approximately the same number of days was required for growth onset in the four transfers (Figure 3a; $P = .09$; Table 2). This indicates either a low chilling requirement that was met already before the November transfer or no rest period and chilling requirement at all in this species. In the other six species, the time required for growth onset decreased from the early transfers to the later ones ($P < .001$, Table 2), but depending on the species, the decrease levelled off during the latest transfers (Figure 3b–g).

The fitted temperature responses of the potential rates of ontogenetic development towards growth onset also showed variation among species (Table 3; Figure 4). *F. vesca* and *L. vulgare*, both rosette plants from meadow habitats, showed generally the highest potential rates (Figure 4a). They were followed by the rhizomatous herbs *O. acetosella* and *H. perforatum* representing boreal forest floor and meadows, respectively (Figure 4a). However, in the lowest test temperature of +5°C, this ranking was slightly changed as *O. acetosella* showed second highest potential rate in that temperature (Figure 4a). The dwarf shrubs *V. vitis-idaea*, *V. myrtillus*, and *L. borealis*, all originating from the boreal forest floor, showed the lowest potential rates of development (Figure 4b).

The results for the interactive effect of state of rest break and temperature on the ontogenetic competence, $C_o(t)$, are shown in Figure S1, and the corresponding estimated parameter values for $C_o(t)$ are reported in Table 3. Based on the experimental results, three dormancy types were identified. The final air temperature responses, drawn by all of the parameter values reported in Table 3, are given in Figure 5 for one representative species of each dormancy type.

In Dormancy Type 1, the ontogenetic competence increases as the state of rest break increases as a result of chilling accumulation, but is fairly independent of the temperature. This type of response is exhibited by *V. myrtillus* and *L. vulgare* (Figures 5a and S2a,b). In this type, there is practically no interaction of previous chilling and temperature on the ontogenetic competence, so that the model developed in the present study (Equations (3) and (4)) reduces into the parallel model (Figure 5a, compare with Figure 1a). In Dormancy Type 2, there is a moderate interaction, as indicated by the moderate response of ontogenetic competence to temperature. This type is represented by *O. acetosella*, *L. borealis*, and *V. vitis-idaea* (Figures 5b and S2c–e). In Dormancy Type 3, represented by *F. vesca*, there is a strong interaction indicated by a steep response of ontogenetic competence to temperature (Figures 5c and S2f). Accordingly, the full potential rate of ontogenetic development is attained even without any previous chilling in high temperatures, whereas the rate of ontogenetic development is zero at that time in low temperatures (S_r = 0%, red curve in Figure 5c). With increased accumulation of chilling ontogenetic development becomes possible in successively lower temperatures (Figure 5c). In all, then, the results obtained for *F. vesca* are a typical case of a strong interaction of state of rest break and the prevailing air temperature in the rate of ontogenetic development towards bud burst (compare Figure 1b).

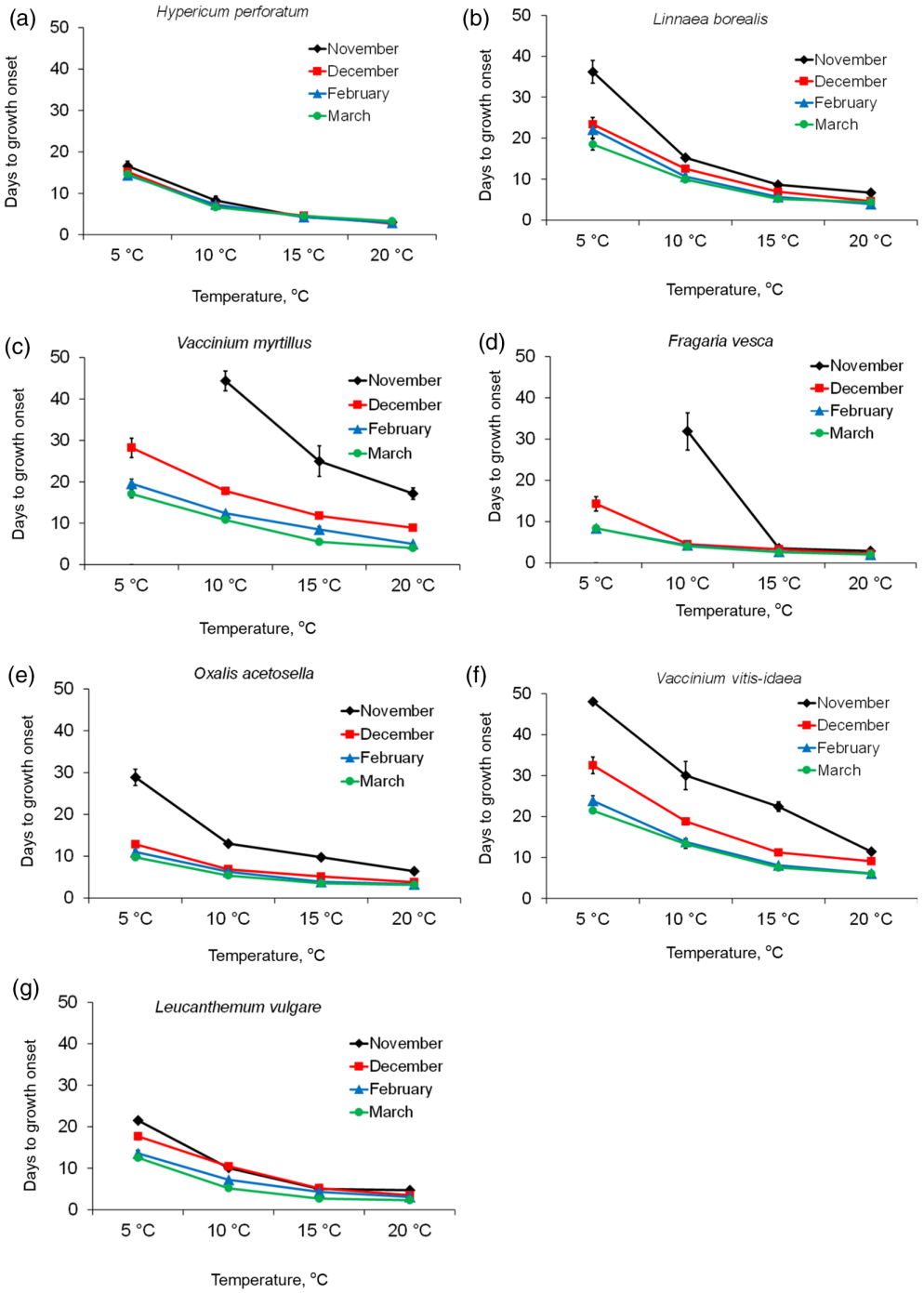

FIGURE 3 The days to growth onset in the seven studied plant species, following transfer from freezer storage at −2.5°C to growth chambers at four different temperatures at four times during the winter. The error bars show the standard error of the means, but they may be obscured by the symbols in some cases

H. perforatum may also represent Dormancy Type 3, but due to the lack of a growth onset experiment in early autumn before November and the low, if any, chilling requirement of this species, the results are uncertain. The fitting algorithm found numerous parameter sets with equally good fit to the data (results not shown). That is, because the chilling requirement of the species is low, any parameter set that results in an ontogenetic competence close to 1 already in the +5°C treatment in November will fit the experimental results equally well. This happens with a large number of parameter sets that combine steep temperature responses of $C_o(t)$ with low values for the C_{crit} parameter. The results for one representative parameter set are shown in Figure S2g.

In the independent test, the model predicted in most cases the observed growth onset with an accuracy of 3–10 days (Figure 6; Table S2). The model prediction was slightly biased, as the predicted growth onset usually took place before the observed one (Figure 6). More importantly, the model prediction failed in the following three

TABLE 2 Two-way ANOVA of the effects of transfer time from a freezer storage to the growth chamber and the growth chamber temperature on the days required for growth onset in the chamber in seven field layer plant species

	Temperature		Transfer time		Temperature × Transfer time	
Species	*F*	*P*	*F*	*P*	*F*	*P*
Fragaria vesca	111.47	<.001	73.61	<.001	43.30	<.001
Hypericum perforatum	426.51	<.001	2.21	.09	1.19	.30
Leucanthemum vulgare	992.87	<.001	125.73	<.001	18.82	<.001
Linnaea borealis	276.34	<.001	33.31	<.001	7.95	<.001
Oxalis acetosella	370.08	<.001	245.92	<.001	34.21	<.001
Vaccinium myrtillus	234.76	<.001	254.03	<.001	17.56	<.001
Vaccinium vitis-idaea	299.36	<.001	166.29	<.001	11.93	<.001

cases: First, no growth onset was observed in the December transfer with *V. myrtillus* after overwintering at any of the three sites, but a growth onset was predicted for all three of them (Figure 6d–f).

TABLE 3 Parameter values of the model of rest break and growth onset estimated by fitting the model (Equations (1)–(7)) to data from the growth chamber experiment

	Parameters of $R_{o,pot}$			Parameters of C_o			
Species	H_{crit}	a	b	C_{crit}	c	d	RMSE (days)
Fragaria vesca	1.74	0.21	11.11	119.9	0.2396	3.216	1.03
Hypericum perforatum	2.30	0.17	14.19	32.2	3.4058	105.112	1.43
Leucanthemum vulgare	2.06	0.30	11.01	33.2	0.0002	0.694	1.61
Linnaea borealis	3.89	0.25	10.76	49.4	0.0113	0.026	1.26
Oxalis acetosella	2.84	0.23	8.89	94.6	0.0142	0.001	0.75
Vaccinium myrtillus	2.81	0.18	14.68	112.0	0.0006	0.032	1.45
Vaccinium vitis-idaea	4.38	0.19	12.71	121.5	0.0133	0.000	1.75

Note. Parameters of the air temperature response of the potential rate of ontogenetic development, $R_{o,pot}$: H_{crit} is the high temperature requirement of growth onset, and *a* and *b* are parameters determining the shape of the sigmoidal temperature response (Equation (1)). Parameters of the model for ontogenetic competence C_o: C_{crit} is the chilling requirement of rest completion, and *c* and *d* are parameters determining the interactive effect of state of rest break and the prevailing air temperature on the ontogenetic competence (see Equations (3) and (4) and Figure S2). The goodness-of-fit of the model fitting is indicated by the RMSE value. Units of the parameters (the parameters *c* and *d* were introduced in the present study; for others, see Hänninen and Kramer (2007) and Hänninen (2016): H_{crit} (arbitrary high temperature unit), *a* ($°C^{-1}$), *b* (°C), C_{crit} (arbitrary chilling unit), *c* ($°C^{-1}$), and *d* (dimensionless).

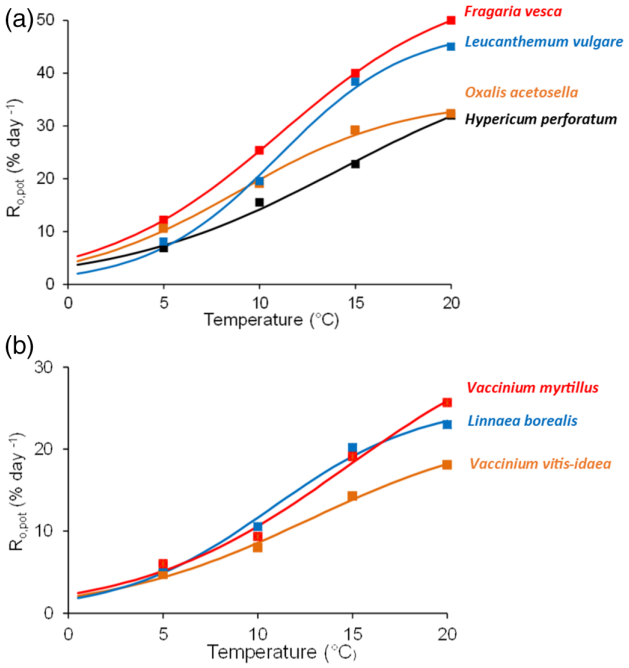

FIGURE 4 The temperature response of the potential rate of ontogenetic development towards growth onset, $R_{o,pot}$, in (a) the four herbaceous and (b) the three dwarf shrub species studied. The responses were determined by fitting Equation (1) to the data from the March transfer in the growth chamber experiment. Note the difference in scale of the vertical axis in the two figures

Second, for the December transfer, a very late growth onset was predicted for *F. vesca* after overwintering in Nåtö, but an early growth onset was still observed with it (Figure 6i; Table S2). This inaccuracy is in striking contrast with the results obtained with the same species after overwintering at the two other sites, where the accuracy of the model prediction was close to the average (Figure 6g,h; Table S2). Third, the growth onset of *H. perforatum* was predicted to occur at the three overwintering sites already before the third transfer, but it was observed only after the transfer to the growth chamber (Figure 6j–l). Because of these exceptional failures, the RMSE varied in the independent test from 9.2 to 19.2 days, and because no bud burst was observed in *V. myrtillus* in the December transfers, it was not possible to calculate the value of RMSE for that species (Table S2).

4 | DISCUSSION

4.1 | Insight into the dormancy phenomena of plants

The results of the present study suggest that the effects of temperature on rest break and subsequent growth onset of plants are more complicated than assumed in the classical dichotomy of the rest (endodormancy) and quiescence (ecodormancy) concepts (Doorenbos, 1953; Fuchigami et al., 1982; Hänninen, 2016; Lang et al., 1987; Romberger, 1963; Weiser, 1970). Based on the present results, it was possible to identify three dormancy types of the plants. Plant species

following the classical dichotomy concept were classified into Dormancy Type 1 (*V. myrtillus* and *L. vulgare*). In the other species, the interaction of previous chilling and prevailing temperature was seen. Species with a moderate interaction were classified into Dormancy Type 2 (*O. acetosella*, *L. borealis*, and *V. vitis-idaea*) and those with a strong interaction into Dormancy Type 3 (*F. vesca*, possibly also *H. perforatum*, but the latter was uncertain due to problems in the model fitting).

The strong interaction included in the Dormancy Type 3 results in dramatic changes in the shape of the temperature response of rate of ontogenetic development during the rest period (Figure 5c). Ontogenetic development takes place during early phases of rest only in temperatures above a high threshold of 12–14°C, but this threshold is lowered as rest progresses. Furthermore, the slope of the curve changes so that during the early phases of rest, the curve is exceptionally steep, but later during rest, the curve resumes a slope more similar to the other dormancy types (Figure 5). In other words, during early phases of rest, the rate of development is close to its maximal rate whenever temperature is high enough to promote any ontogenetic development, but later, the rate of development increases with rising temperature on a broad temperature range.

The strong interaction found for *F. vesca* belonging to Dormancy Type 3 was seen also in the growth onset percentages for that species in the November transfer: 0%, 70%, 100%, and 100% for the forcing temperatures of +5, +10, +15, and +20°C, respectively (Table S1). The growth onset percentage was in the November transfer at +5°C 0% also in *V. myrtillus*. However, in that species, the failure of growth onset at +5°C in November transfer was not caused by the interaction, because a reduced growth onset percentage was observed in the November transfer in that species also at the higher temperatures (Table S1). These findings are in accordance of *V. myrtillus* being classified in Dormancy Type 1. In *V. vitis-idaea*, the growth onset percentages were in the November transfer low in the two lowest temperatures (Table S1). This is in accordance with the moderate interaction of that species classified into Dormacy Type 2.

One can only speculate on the ecological and physiological background of the dormancy types found in the present study. *F. vesca* and less conclusively *H. perforatum* were classified into Dormancy Type 3. They are both meadow plants, but so is also *L. vulgare*, which was classified into Dormancy Type 1. Accordingly, the dormancy types do not appear to have any relation to the habitat of the species. However, the change of the air temperature response involved in Dormancy Type 3 (Figure 5c) prevents a premature growth onset during mild spells (0–10°C) in winter, thus avoiding damage during subsequent frost periods (Hänninen, 2016). Based on this reasoning, two hypotheses can be presented. Ecologically, it can be hypothesized that species belonging to Dormancy Type 3 are common in locations with relatively maritime climates, where the winters are in general mild, but intermittent frost periods still occur. However, the only species that was in the present study clearly found to belong to Dormancy type 3, *F. vesca*, is native to a large part of the Northern hemisphere, so our limited findings do not support the hypothesis. Physiologically, it can

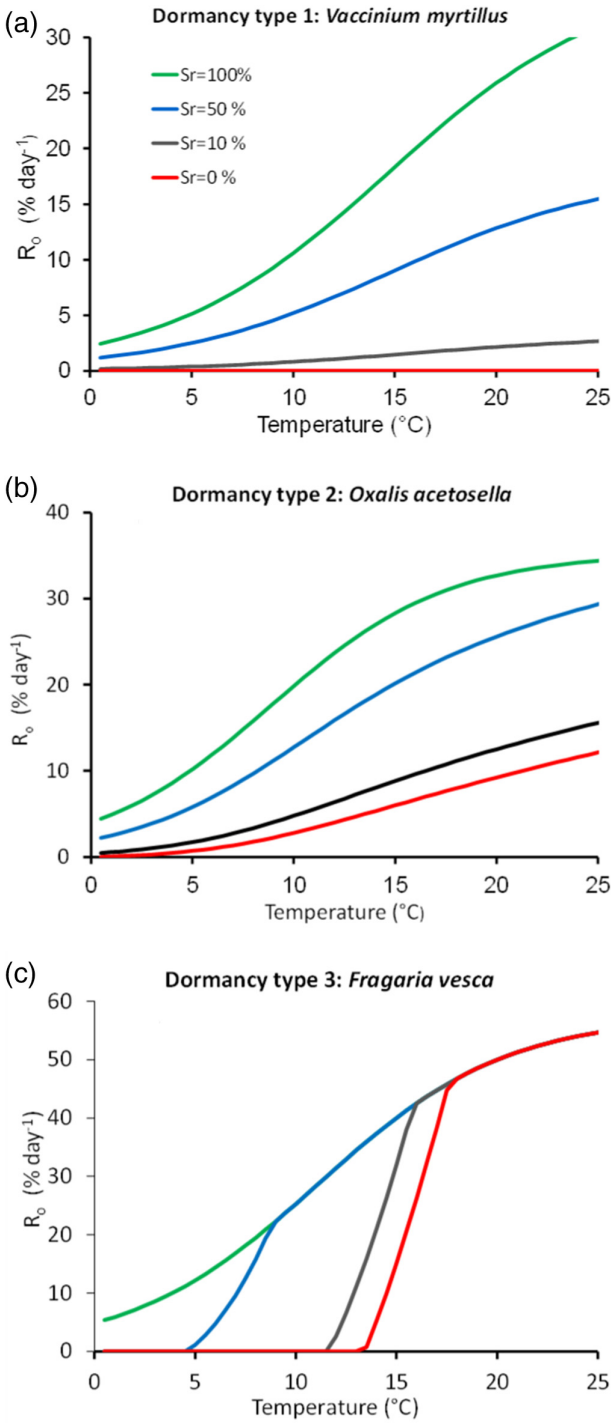

FIGURE 5 The temperature responses of the rate of ontogenetic development towards growth onset of three of the studied plant species, exemplifying the three corresponding dormancy types identified in the study. The responses are shown for four phases of rest break indicated by the value of state of rest break, $S_r(t)$.
(a) Dormancy Type 1, as exemplified by *Vaccinium myrtillus*.
(b) Dormancy Type 2, as exemplified by *Oxalis acetocella*.
(c) Dormancy Type 3, as exemplified by *Fragaria vesca*. Note the different scale of the vertical axis in the different figures

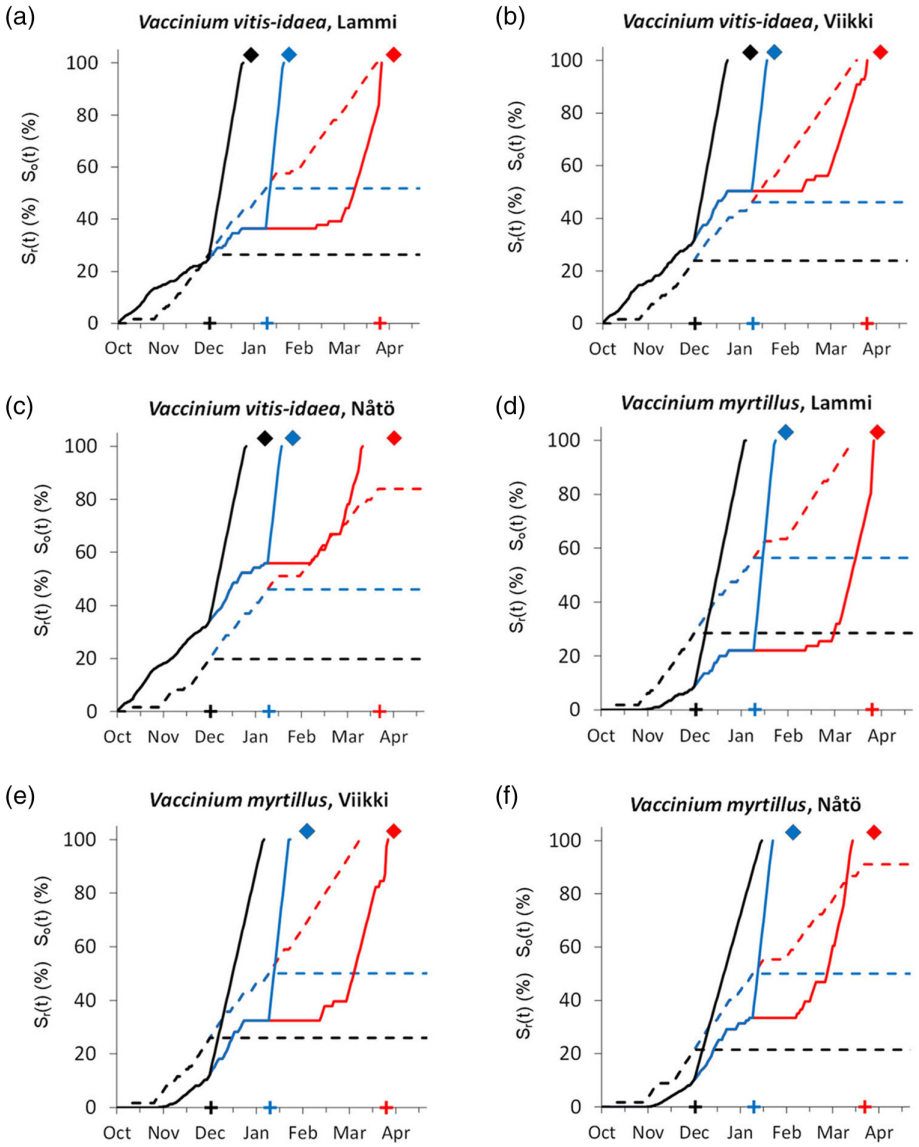

FIGURE 6 A test of the rest break and growth onset model developed in the present study, using independent data of growth onset collected with four plant species. The experimental plants overwintered first in natural conditions at three geographical locations with different climatic conditions (Lammi, Viikki, Nåtö) and were then transferred to growth chambers at +10°C at three occasions indicated by the crossbars on the horizontal axis. The predicted state of rest break, $S_r(t)$, is indicated by the dashed curves. The end of the curve at $S_r(t)$ = 100% indicates the predicted rest completion (meeting of the chilling requirement), but in many cases, the chilling requirement was not met, and the curve of $S_r(t)$ reached a plateau at the time of the respective transfer to the growth chamber, where no further chilling took place. The predicted state of ontogenetic development, $S_o(t)$, is indicated by the continuous curves. The end of the curve at $S_o(t)$ = 100% indicates the predicted growth onset; the observed growth onset is marked by a diamond. Black, blue, and red symbols indicate the three transfers in December, January, and April, respectively. Note that the blue and red curves are used only after the corresponding transfer, so that until the first transfer, the black curve is used for all transfers, and between the first and second transfer, the blue curve is used also for the third transfer

be hypothesized that as the plants belonging to Dormancy Type 3 avoid a premature growth onset during mild spells in winter, they maybe just before and at the time of growth onset less frost hardy than the plants belonging to the other two dormancy types.

Our findings show that the concept of "unfavourable environmental factor" included in the classical quiescent (ecodormancy) concept is not unambiguous (Hänninen, 2016). This notion has an important implication: Whenever the interaction of physiological and environmental factors suggested by Vegis' (1964) conceptual model is present, it is not possible to divide the dormancy status categorically into the two types of rest and quiescence. This notion is in accordance with the current understanding of the physiological and molecular basis of plant dormancy, which emphasizes the dynamic and quantitative nature of the dormancy mechanisms, rather than strict categories and limits between dormancy phases (Cooke et al., 2012).

Our finding has also an important methodological implication: Whenever the interaction examined in the present study is present,

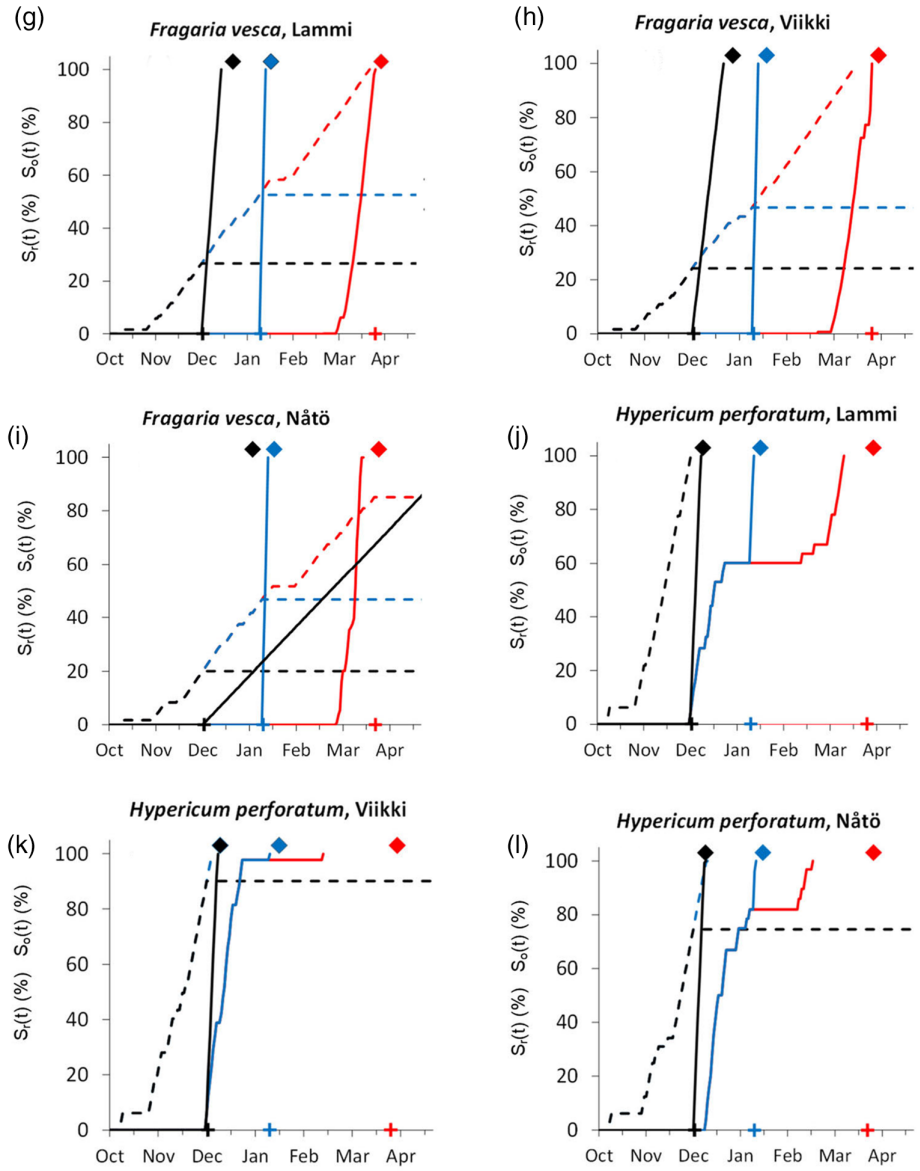

FIGURE 6 (Continued)

the results of any chilling–forcing experiment addressing the chilling requirement depend on the forcing temperature applied. Studies applying high forcing temperatures will imply lower chilling requirements than those applying low forcing temperatures. For this reason, Vegis' (1964) conceptual model is important also for practical forestry and horticulture.

Recently, Hochberg, Rockwell, Holbrook, and Cochard (2018) introduced for studies of plant water relations a plant–environment interaction basically similar to the one we are now suggesting for bud dormancy release. These two novel approaches may be manifestations of an upcoming general paradigm change in plant biology. The interaction of environmental and physiological factors may be involved in many such phenomena that have until now been considered simply as plant traits without any considerable effects of environmental factors.

4.2 | Process-based plant phenology modelling

Hänninen (1990) made the first attempt to introduce the interactive conceptual model of Vegis (1964) into the process-based phenology models. More recently, Hänninen (2016) provided a new model formulation including Vegis' (1964) conceptual model. However, in both of these studies, the models were used only for theoretical simulations illustrating the implications of Vegis' (1964) conceptual model, without parameterizing the model for any plant species. In the DORMPHOT model of Caffarra, Donnelly, and Chuine (2011) developed for *B. pubescens*, a complicated interaction of photoperiod, chilling, and prevailing air temperature is assumed. In their model, long photoperiods shift the air temperature response of rate of ontogenetic development into lower temperatures, and chilling affects the extent of this shift. This interaction is in broad accordance with Vegis' (1964) conceptual model, but no reference to his study was given by

Caffarra et al. (2011). Thus, to our knowledge, our study is the first one where Vegis' (1964) conceptual model is addressed explicitly and operationally in quantitative plant phenology modelling.

The model development in the present study was based on one growth chamber experiment. It goes without saying that the present results should be interpreted with care, and further experiments are needed to test the conclusions. However, in most cases, the model predicted the observed bud burst with an accuracy of 3–10 days in an independent test whose results were not used for formulating the model. This suggests that our model roughly describes real physiological phenomena of the plants. In a few cases the model failed, however, rather than completely rejecting the model, these deviations may indicate the need to adjust the model based on additional experimental work (Hänninen, 2016).

For instance, the model predicted for *F. vesca* that attaining the state of rest of $S_r(t)$ = 20.0% at the time of the first transfer from Nåtö would not facilitate a regular rapid ontogenetic development towards growth onset at +10°C in the growth chamber, however, in contrast to that prediction, growth onset was observed in the growth chamber after the transfer (Figure 6i). In the corresponding transfer from Viikki with $S_r(t)$ = 24.2%, the development was accurately predicted (Figure 6h). Thus, a difference of 4.2% in the value of $S_r(t)$ had a major effect to the model performance. This comparison suggests that the parameters of the model for rest break (Equation (5)) and/or those of the model for ontogenetic competence (Equations (3) and (4)) should be reconsidered with further experimental work.

The model for rest break (Equation (5)) would be the first one to be addressed. It was not possible to determine the air temperature response of rate of rest break as our experiment only included one chilling temperature. Accordingly, we needed to use a rough approximation of that response. Uncertainties in the rest model were also probably causing the failure of the model with *V. myrtillus*: Growth onset was predicted to occur for all three overwintering locations in the growth chamber also after the shortest chilling in the first transfer, but unlike in the later transfers, no growth onset took place after the first transfer for any of the three overwintering locations (Figure 6d–f).

We used a low chilling temperature (−2°C) in order to make sure that no ontogenetic development towards growth onset takes place already in the chilling conditions before transfer to the forcing conditions. Sometimes, only temperatures above zero are considered as effective in chilling (Hänninen, 2016). However, in our study, the DBB values decreased from the early to the late transfers, and the differences in the DBB values between the last two transfers were small (Figure 3). These findings show that in our study, −2°C was effective in rest break and that the chilling requirement was met at the time of the last transfer in March.

Vegis' (1964) interactive conceptual model provides a potential explanation to many earlier paradoxical results concerning the timing of rest completion in boreal and temperate trees, which have hampered the modelling of tree seasonality and also caused a major uncertainty to the projections of the ecological effects of climate change (Hänninen, 2016). These considerations, together with the support for Vegis' (1964) conceptual model obtained in the present study and earlier in studies with *Betula* species (Caffarra et al., 2011; Junttila & Hänninen, 2012) suggest that the present paradigm of the dichotomy of the physiological and environmental effects on plant dormancy needs to be replaced in plant phenology modelling by a new one allowing also the interaction of these two. This conclusion addressing the whole plant modelling is in accordance with the current understanding of the molecular mechanisms of plant dormancy, which emphasizes the dynamic and quantitative nature of the dormancy mechanisms, rather than strict categories and limits between dormancy phases (Cooke et al., 2012).

The plant phenology models addressing both rest break and ontogenetic development have been applied mainly with trees (Chuine et al., 2013; Hänninen, 2016) and in a few cases with dwarf shrubs (Pop et al., 2000; Van Wijk et al., 2003) and herbaceous crop cultivars (Tanino & Wang, 2008). In the present study, we broaden the scope of the modelling to native herbaceous plants. The results suggest that the studied herbaceous plants have similar dormancy phenomena, such as chilling requirement of rest completion, as the woody plants studied earlier. The simulations from the independent model test of the present study further suggest that the chilling requirement of the herbaceous plants may be so large that it is not met in natural conditions until quite late in the spring. This is seen in the simulations for the *F. vesca*, as the value of the variable state of rest break remained below 50% in the December and January transfers (Figure 6g–i).

4.3 | Conclusions

We introduced into process-based quantitative plant phenology modelling a novel aspect, which is based on an old, largely neglected conceptual model. The novel aspect caused only a minor change in the mathematical model formulation, but biologically, it introduced a major change in the conceptualization and quantification of the dormancy phenomena of the plants. The earlier models were mainly based on a conceptual dichotomy of the dormancy being caused either by the physiological condition of the bud or by the prevailing environmental conditions. While allowing this old concept as one special case, our new formulation introduces the idea of dormancy being regulated as an interaction of the physiological and environmental factors. The model was parameterized with growth chamber experiments for seven boreal field layer plant species and tested with independent experiment with four species. We also broadened the scope of the modelling into native herbaceous plants. Based on the occurrence and the strength of the interactive effect, the results facilitated the identification of three novel dormancy types of the plants. Together with a recent study addressing plant water relations, our study suggests that interaction of environmental and physiological factors may be involved in many such phenomena that have until now been considered simply as plant traits without any considerable effects of environmental factors.

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AUTHOR CONTRIBUTIONS

R.L. had the main responsibility in all phases of the study. He invented and formulated the novel model. H.H. had a major contribution in designing the experiment and in writing the manuscript. T.S. and H.Å. contributed in performing the experiment and commented on the manuscript. R.Z. carried out the statistical analyses and commented on the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

Figure S1. Experimental field set-up used in the independent test of the model of rest break and growth onset. At each of the three overwintering sites, 30 potted plants were located in baskets directly on the ground so that during winter they were covered by snow, if any. The baskets inhabiting also other plants are seen on the right, the boxes on the left belong to another experiment

Figure S2. Effects of prevailing temperature and state of rest break (previous chilling) on the ontogenetic competence as calculated by the equations 3 and 4 for the seven examined plant species with the parameter values reported in Table 3. Based on the strength of the interaction between temperature and the state of rest break in determining the ontogenetic competence the species are grouped into three dormancy types. In each panel the strength is visualized by the slope of the curve with increasing temperature values to the left at relatively small values of state of rest break. Dormancy Type 1: No interaction. The ontogenetic competence is determined exclusively by state of rest break. Dormancy Type 2: moderate interaction. At low values of state of rest break ontogenetic competence increases moderately with increasing temperature. Dormancy Type 3: strong interaction. At low values of state of rest break ontogenetic competence increases strongly with increasing temperature

Table S1. Growth onset percentages observed for the seven examined plant species in the treatments of the study. The months indicate the transfer time from chilling to forcing conditions and the temperatures the forcing temperature applied.

Table S2. Predicted and observed timing of growth onset in an independent test of the model of rest break and growth onset developed in the present study. The column for location indicates the location where the plants were overwintering before the transfer to the growth chamber at 10 °C. The column for transfer indicates the time of the transfer to the growth chamber: December = 14 December 2011 (Nåtö), 15 December 2011 (Viikki, Lammi); January = 21 January 2012 (Nåtö) 22 January 2012 (Viikki, Lammi); April = 3 April 2012 (Nåtö), 6 April 2012 (Lammi and Viikki). In the columns for growth onset, Dec indicates December 2011 and the other symbols the

indicated month for 2012. In the error column, the minus (–) and plus (+) signs indicate too early and too late model predictions, respectively, as compared with the observation. * indicates that no growth onset was observed. The RMSE of the model prediction was 19.2, 13.1, and 9.2 days for *F. vesca*, *H. perforatum*, and *V. vitis-idaea*, respectively. For *V. myrtillus* the RMSE could not be calculated since in the December transfers no growth onset was observed in it.

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