Plant Phenology Models

Phenology

Chuine, Isabelle; de Cortázar-Atauri, Iñaki García; Kramer, Koen; Hänninen, Heikki

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Chapter 14
Plant Phenology Models

Isabelle Chuine, Iñaki García de Cortázar-Atauri, Koen Kramer, and Heikki Hänninen

Abstract In this chapter, we provide an overview of plant phenology modeling, focusing on mechanistic phenology models. After a brief history of plant phenology modeling, we present the different models, which have been described in the literature and highlight the main differences between them, i.e. their degree of complexity and the different types of response function to temperature they use. We also discuss the different approaches used to build and parameterize such models. Finally, we provide a few examples of applications mechanistic plant phenology models have been successfully used for, such as the modeling of frost hardiness, forest growth and distribution, evolutionary dynamics of phenological traits, and the reconstruction of temperature during the last millennium.

14.1 An Overview of Plant Phenology Models

The key importance of seasonal timing for plant growth, reproduction, and survival has surged a growing number of ecologists and agronomists to understand and model how environmental conditions control phenology in order to predict the

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I. Chuine (✉)
CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Montpellier, France
e-mail: isabelle.chuine@cefe.cnrs.fr

I. G. de Cortázar-Atauri
AGROCLIM INRAE, Avignon, France
e-mail: inaki.garciadecortazar@inrae.fr

K. Kramer
Forest Ecology and Forest Management Group, Wageningen University, Wageningen, The Netherlands

Land Life Company, Amsterdam, The Netherlands
e-mail: k.kramer@landlifecompany.com

H. Hänninen
State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Hangzhou, China
e-mail: hhannin@zafu.edu.cn

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impacts of climate change on agriculture and natural ecosystems. Phenology models have become a key component of different kinds of models simulating crops yield (Nissanka et al. 2015), Earth systems (Dahlin et al. 2015), population dynamics (Anderson et al. 2013; Maino et al. 2016; and see also Chap. 15 in this volume), species distribution (Chuine 2010), and evolutionary dynamics (Donohue et al. 2015; Duputié et al. 2015; Gaüzere et al. 2020).

14.1.1 The Different Types of Phenology Model

Phenology modeling has a long history starting in 1735 with a publication by De Reaumur (1735) which suggested that differences between years and locations in the date of phenological events could be explained by differences in daily temperatures from an arbitrary date to the date of the phenological event considered. He thus introduced the concept of degree-day summation. While this is still the most important assumption in plant phenology modeling, major advances took place in the late twentieth century for two main reasons: (i) the revolution in computer science, and (ii) concerns about global climate change, which has major impacts on phenological events (Cleland et al. 2007; Inouye 2022).

Most plant phenology modeling studies have focused on leaf unfolding and flowering, and much fewer on fruit maturation, growth cessation or leaf senescence. This is because (1) leaf unfolding and flowering are the most widely observed phenophases, (2) the timing of these events can be observed more accurately (Denéchère et al. 2019; Liu et al. 2021), and (3) leaf unfolding is very important for primary production (Piao et al. 2007; Richardson et al. 2010) while flowering largely determines plant reproductive success (see Sect. 14.4).

Three main types of phenology models exist: analytical, statistical, and mechanistic. Analytical phenology models are mathematically tractable and focus on the cost/benefit tradeoff of producing leaves to optimize resource acquisition (Kikuzawa 1991, 1995a, b, 1996; Kikuzawa and Kudo 1995) and are designed to understand the evolution of leaf lifespan strategies in trees, rather than the annual variation in plant phenology. Statistical phenology models use statistical techniques such as regression and classification to relate the timing of phenological events to climatic factors. Their parameters are estimated from data using various statistical fitting methods. Most of these models do not consider specific biological processes, and can be simple correlations with average temperature in different periods of the year (Boyer 1973; Spieksma et al. 1995; Emberlin et al. 1997; Ruml et al. 2012). Other models are more complex such as the Spring Indices Models (Schwartz and Marotz 1986, 1988; Schwartz 1997; Schwartz et al. 2013), models based on Partial Least Square regressions (particularly suited to autocorrelated data), and models based on semi parametric or modified survival models (Terres et al. 2013; Allen et al. 2014; Betancourt 2022). We do not comment more on these types of models in this chapter, which is focused on the third type of model, i.e. mechanistic models, which are the most numerous in the literature. However, one needs to note that some models can be considered as intermediate between statistical and mechanistic as they use some response functions to environmental cues to compute some covariates which are characteristic of mechanistic models (Allen et al. 2014).

Mechanistic phenology models formally describe known or hypothetical cause-effect relationships between physiological or gene regulation processes and some driving factors in the plant's environment. A new relationship is introduced in a mechanistic model only if information on its impact on the process is available. Parameters of mechanistic models have physical dimensions that can, in principle (see Sect. 14.3), be measured directly instead of being estimated by statistical inference, although this is not always possible (see Sect. 14.3.1). The structure of mechanistic models is usually based on systems theory rather than mathematical analyses of statistical inference (Hänninen and Kramer 2007; Chuine 2010). The following paragraphs provide a detailed overview of hypotheses of mechanistic models.

14.1.2 Hypotheses and Structure of Mechanistic Phenology Models

Mechanistic phenology models are deeply grounded on experimental work designed to decipher how environmental conditions regulate the development of vegetative and reproductive organs. From experimental evidence, we know at least three things on this regulation. First, in perennials naturally, bud endodormancy, i.e. the period during which dormancy is caused by internal factors (Lang et al. 1985) is naturally broken by cool temperatures (from slightly negative to around 12 °C, Vegis 1973; Sarvas 1974; Hänninen 1990; Caffarra et al. 2011a). Cool temperatures are also needed for annual plants during the vernalization period (Satake 2010). Second, warm temperatures (positive temperatures) accelerate cell growth during ecodormancy, i.e. the period during which dormancy is caused by external factors, and subsequent development of leaves, flowers and fruits (Lamb 1948; Sarvas 1972, 1974; Landsberg 1974; Campbell and Sugano 1975; Lang et al. 1985; Caffarra et al. 2011b). Third, photoperiod may interact with the temperature response during ecodormancy in perennials by compensating for a lack of chilling during endodormancy, but also during stem elongation in grasses. Large differences in the sensitivity of bud break to photoperiod exist between species and studies (Heide 1993a, b; Kramer 1994b; Falusi and Calamassi 1996; Caffarra et al. 2011a; Flynn and Wolkovich 2018). The effect of photoperiod has been particularly well demonstrated for *Fagus* species (Wareing 1953; Heide 1993b; Myking and Heide 1995; Basler and Körner 2014; Fu et al. 2019; Flynn and Wolkovich 2018; Osada et al. 2018) and winter crops like wheat (Wang and Engel 1998).

Most differences between mechanistic phenology models come from the number of different phases they represent, the response functions to environmental variables they consider for each phase, and the occurrence of interactions between these

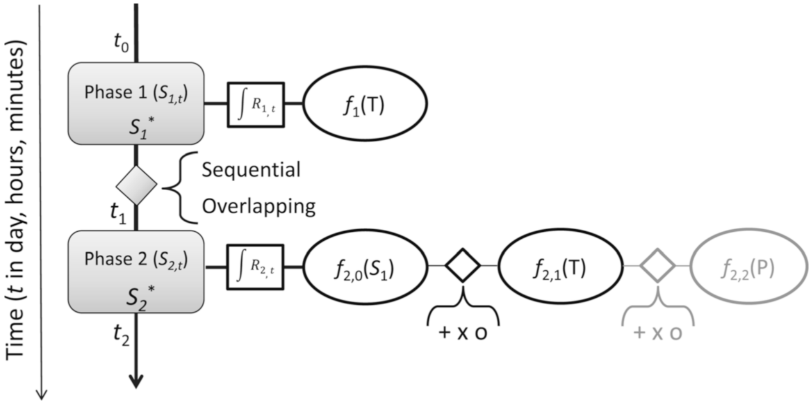

Fig. 14.1 Structure of mostly used mechanistic 2-phase phenology models. *S* is the state of development, *S** are critical states of development corresponding to the end of each phase of development, *R* are the rates of development, *f* are response functions to environmental cues: temperature (T) and photoperiod (P), which can be combined with an addition, multiplication, or composition. Results of *f* functions and their combination are integrated through time to determine the state of development. Phase 2 can either follow phase 1, starting at t_1 determined by S^*_1, or overlap with phase 1. Results of response functions of phase 2 to environmental cues ($f_{2,1}$ and $f_{2,2}$) can be affected by the state of development of phase 1

phases (Fig. 14.1). Development is represented by a state variable, *S* for development Stage, which is the integration of development rates (*R*) over time (in steps of days, hours or minutes) from a start date t_0, which are a function of some environmental cues. The general structure of mechanistic phenology models for one specific development phase is the following:

$$t_n \text{ such that } S_{n,t} = \sum_{t_{\mathrm{n}-1}}^{t_n} R_{\mathrm{n,t}}(Z) = S_n{}^* \tag{14.1}$$

where *n* a development phase (e.g., endodormancy, ecodormancy, fruit maturation), $S_{n,t}$ is the state of development on day *t* in phase *n*; t_n is the end of phase *n* and t_{n-1} the end of phase $n-1$. $R_{n,t}$ is the rate of development during phase *n* on day *t* which is a function of one or a set of daily or hourly environmental variables *Z* (e.g., temperature, photoperiod, water potential), and S_n* the critical state required to reach t_n. Virtually any phenology model can fit into this framework. For example, the growing degree-day model also called Thermal Time model or Spring Warming model, the simplest plant phenology model, requires only three parameters and can be written as a one-phase model as follows:

$$R_{1,t}(x_t) = \begin{cases} 0 & \text{if } x_t \leq T_b \\ x_t - T_b & \text{if } x_t > T_b \end{cases} \tag{14.2}$$

Table 14.1 List of the different phenology models described in the literature

Phenophase	Plant types	Model name
Ecodormancy	Crops	Growing Degree Days/Thermal Time[1], Photothermal Time[2], Triangular Growing Degree Hour model[3], Robertson model[4], Sinclair model[5], Soltani model[6], Hartkamp model[7]
	Grapevine	Sinusoidal-parabolic model[8], Action Days model[9]
	Fruit trees	Growing degree Hours[10]
	Red osier Dogwood	Kobayashi and Fuchigami model[11]
Endodormancy	Fruit trees	Asymcur[12], Chilling Hour[13,14], Dynamic model[15,16], Positive Utah[17], Smoothed Utah[18]
Endodormancy + Ecodormancy	Trees	Alternating[19,20], Bidabé[21], Deepening Rest [22], Four Phases[23,24], Hänninen model[25,26], Kramer model[27], Parallel[28,29], PGC[30], PGCA[31], PhenoFlex[32], PIM model[33], Sequential[34,35], Unichill[36], UniForc[37], Unified[38]
	Crops	Biological Days[39]
Dormancy induction + Endodormancy + Ecodomancy	Trees	DormPhot[40]
Fruit maturation	Trees	Asymmetric unimodal[41,42,43]
Leaf senescence	Trees	Delpierre model[44]
	Land surface	White model[45]

1, de Reaumur (1735) in Wang (1960); 2, Masle et al. (1989); 3, Robertson (1968); 4, Sinclair et al. (1991); 5, Hammer et al. (1993); 6, Soltani et al. (2006); 7, Hartkamp et al. (2002); 8, Riou (1994); 9, Pouget (1972); 10, Anderson et al. (1986); 11, Kobayashi and Fuchigami (1983a); 12, Richardson et al. (1982); 13, Bennett (1949); 14, Weinberger (1950); 15, Erez et al. (1990); 16, Fishman et al. (1987); 17, Linsley-Noakes et al. (1995); 18, Bonhomme et al. (2010); 19, Cannell and Smith (1983); 20, Kramer (1994b); 21, Bidabé (1967); 22, Kobayashi et al. (1982); 23, Hänninen (1990); 24, Vegis (1964); 25, Hänninen (1990); 26, Hänninen (1995); 27, Kramer (1994b); 28, Hänninen (1987); 29, Landsberg (1974); 30–31, Gaüzere et al. (2017); 32, Luedeling et al. (2021); 33, Schaber and Badeck (2003); 34, Linkosalo et al. (2008); 35, Richardson et al. (1974); 36, Hänninen (1987); 36–37, Chuine et al. (1999); 38, Chuine (2000); 39, Hunt and Pararajasingham (1995); 40, Caffarra et al. (2011b); 41, Wang and Engel (1998); 42, Yin et al. (1995); 43, Yan and Hunt (1999); 44, Delpierre et al. (2009); 45, White et al. (1997)

where x_t is daily mean temperature, $t_{n-1} = t_0$ is the day on which summation starts, T_b is the summation threshold temperature, and S_I* is the familiar degree-day sum required to complete the phenophase at t_1.

Several phases can be modeled in a single model composed of several sub-models each describing a specific phase such as dormancy induction, endodormancy, ecodormancy, etc. (Fig. 14.1).

Two-phase models for leaf unfolding and flowering typically consider endodormancy in addition to ecodormancy (e.g., the Sequential, Parallel, Alternating, Deepening Rest models, Table 14.1, Fig. 14.1). An important difference between two-phase models is the relationship between the endodormancy phase and the ecodormancy phase: phases either follow each other or overlap. In the latter case, the endodormancy status affects the ecodormancy status and this interaction has been formalized in different ways (Hänninen 1990; Kramer 1994a, b; Chuine 2000; Zhang et al. 2022, 2023).

Three-phase models for leaf unfolding or flowering typically describe the dormancy induction phase in addition to endodormancy and ecodormancy phases (Dormphot model). The Four-phase model for leaf unfolding describes a dormancy induction and an ecodormancy phase, but splits the latter into two phases (true rest and post-rest). In most models, phase n follows sequentially phase $n-1$, but in some models the processes of the different phases can overlap. For instance, a parallel model allows ontogenetic development (which is the typical process of ecodormancy) to take place at high temperatures even before endodormancy has completed.

For herbaceous species, especially crops, models can be more or less complex depending on the number of phases they take into account as well, but typically they consider a germination phase that depends on temperature and soil moisture, a flowering phase that depends on temperature, precipitation and photoperiod, and the maturation phase that depends on temperature (Wang and Engel 1998).

Whatever the species, the developmental responses to temperature have been described by various types of functions, linear and nonlinear (Fig. 14.2). Response functions to other cues have been introduced in phenology models for plants, especially for photoperiod (Schaber and Badeck 2003; Caffarra et al. 2011b; Gaüzere et al. 2017; Kramer et al. 2017), but they are similar to functions already used for temperature. The effects of temperature and photoperiod on bud development seem to interact in a complex way (e.g. Brelsford and Robson 2018; Brelsford et al. 2019). For example, in the model of Caffarra et al. (2011b), which is based on experimental results, photoperiod compensates for a lack of chilling temperature during endodormancy and the mid-response photoperiod of the sigmoid response function varies with the amount of chilling received.

The variety of model assumptions and formulations called for a consistent notation and for attempts at unification. This was started by Hänninen (1987) who divided models in two categories (“sequential” and “parallel”) based on their ecophysiological distinctions. Later on, Hänninen (1990, 1995) introduced a unifying formulation for several model types, and Kramer (1994a, b), Chuine (2000), Hänninen and Kramer (2007) and Kramer et al. (2017) broadened the approach using fitting procedures to select between different forms of model structure and response functions.

As reviewed in this chapter, traditionally, mechanistic tree phenology models have been used for temperate and boreal trees. However, recently the scope of the models has broadened to cover more southern trees too. Chen et al. (2017) first proposed to use a numerical approach (see Sect. 14.3.1) with observational phenological records to develop a model for *Melia azedarach*, a tree species of tropical origin, and apply the model in subtropical and tropical conditions in eastern China (but see Supplementary Material in Zhang et al. 2022). More recently, Zheng et al. (2021, 2022, 2023) took an experimental approach (see Sect. 14.3.2) to develop

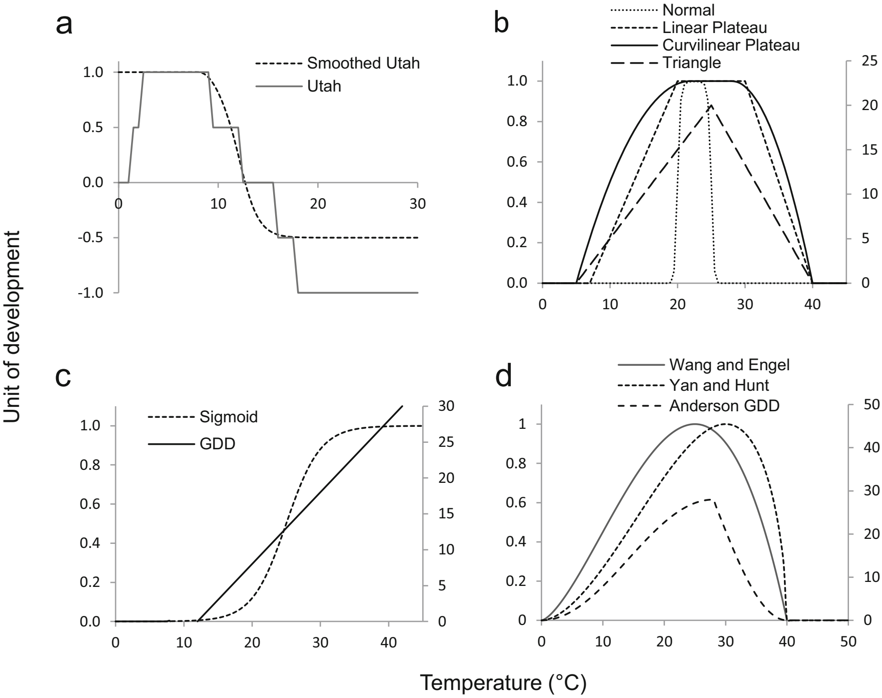

Fig. 14.2 Examples of response to temperature during dormancy induction, endodormancy and ecodormancy. (**a**) Utah and smoothed Utah response functions; (**b**) Normal, triangular, linear plateau and Curvilinear plateau response functions; (**c**) sigmoid and growing degree-day response functions; (**d**) Wang and Engel, Yan and Hunt and Anderson response functions. See Table 14.1 for the references. (Reproduced with permission from Chuine et al. 2013)

process-based phenology models for several subtropical tree species. Their studies based on experimental work revealed that higher temperatures have a chilling effect in the subtropical than in the more northern trees (Jewaria et al. 2021).

To facilitate the development and the parameterization of mechanistic phenological models, different software packages have been developed, e.g. the user friendly PMP (Phenology Modeling Platform) freeware (http://www.cefe.cnrs.fr/en/logiciels/ressources-documentaires), and the Phenor R package (Hufkens et al. 2018).

14.2 Molecular Phenology Models

The last twenty years, there has been major advances in our understanding of molecular–genetic pathways of environmental regulation of plant development (Chiang et al. 2021; Lloret et al. 2022; Satake et al. 2022; Wang and Ding 2023).

As a result, there is increasing potential to incorporate molecular data into phenology models. Although molecular phenology models' structure is not necessarily different from other mechanistic models, their specificities deserve special attention. Molecular phenology is defined by Kudoh (2016) as 'the study of the seasonal patterns of organisms captured by the techniques of molecular biology'. Therefore, molecular phenology refers to the seasonal variations of gene expression, epigenetic modifications, and quantities of proteins, metabolites and other molecules. Molecular phenology models are very recent and are gaining a lot of attention for several reasons. First, they can be developed faster than other models as they do not require long time series of data (one or two years of gene expression data can be sufficient) and the cost of such data has decreased substantially in the last two decades. Second, they allow testing complex hypotheses on the regulatory network of genes involved in plant development under both natural and controlled conditions, and have thus a higher potential to increase our understanding of the regulation of plant development by environmental conditions. For example, Satake et al. (2013) identified the temperature-dependent transcriptional regulation of the vernalization specific gene AhgFLC and the floral integrator gene AhgFT in *Arabidopsis halleri*. More precisely, they showed that the production rates of both gene transcripts increase with temperature, but more rapidly for AhgFLC than AhgFT, while the degradation rate of AhgFLC decreases and that of AhgFT increases with temperature. Based on the response to temperature of the transcription of only two genes, the authors were able to predict the flowering time of *Arabidopsis halleri* they observed in several places in Japan but also in different controlled conditions. The first molecular phenology model was developed by Aikawa et al. (2010) using a 2-year census of the expression of a temperature-dependent flowering-time gene, AhgFLC, in a natural population of perennial *Arabidopsis halleri*. Later on, Nagano et al. (2012) developed a molecular phenology model using transcriptome data for rice raised in the field. Other molecular phenology models have been published since by Satake et al. (2013), Kudoh (2016), and Mochida et al. (2018). Since molecular phenology models only differ from other phenology models by the phenological variables used, biological data *vs.* molecular data, they can be either statistical models (e.g. Nagano et al. 2012) or mechanistic models (e.g. Satake et al. 2013).

14.3 Methodological Considerations

Mechanistic phenology models need to be first calibrated and then validated. Because phenology models are used to predict future phenology, whether over the coming year (e.g., for orchard management) or over the next century (e.g., for global warming impact assessment), model validation is an essential second step. Cross-validation is an adequate testing method (Chatfield 1988) by which the model is tested by comparing its predictions to observations not used in model fitting. However, this method is data-hungry and it is not always possible to split the dataset into two parts, one to fit the model, the other to test its prediction accuracy. In such cases, one can resort to “leave one out” (or jackknife) cross-validation (Stone 1977; Häkkinen 1999) or test-train-validate methods applied in machine learning (e.g., Fabris and Freitas 2019).

Two approaches are used to estimate parameter values: the experimental approach that tries to measure the response of development to different cues, temperature, photoperiod, water availability under controlled conditions; and the numerical approach, which uses numerical techniques to determine optimal parameter values from combined phenological and environmental time series.

14.3.1 The Experimental Approach

The experimental approach consists in carrying out experiments in order to analyze the underlying mechanisms of phenological responses, one mechanism at a time (Wareing 1953; Samish 1954; Vegis 1964, 1973; Perry 1971). A growing number of studies have been following this method during the last two decades (Caffarra et al. 2011a; Baumgarten et al. 2021; Zheng et al. 2021; Zhang et al. 2022, 2023). This method traces back to the pioneering work of Sarvas (1972) who determined experimentally the temperature response of development rate during ecodormancy, using observations of meiosis in pollen mother-cells of several forest tree species. He found that *developmental time*, i.e. the average time between two meiotic phases, declines exponentially with increasing temperature. Sarvas (1974) also determined the progress of dormancy release indirectly using regrowth tests where seedlings were incubated at growth-promoting temperatures following a period of chilling. Both the chilling duration and temperatures were varied systematically. Sarvas found that the duration of chilling required for completion of endodormancy was shortest at +3.5 °C, and concluded that the rate of development (rate of dormancy release) was highest at this temperature. These results led to the triangular temperature response (peaking at 3.5 °C) proposed for the rate of dormancy release (Fig. 14.2b).

Later on, experimental work served (i) to elucidate how different cues were regulating bud, leaf, flower, and fruits development, and thus determine which type of response function should be used and how each cue was interacting with the others (e.g. Hänninen 1990; Caffarra et al. 2011a; Chiang et al. 2021); but also (ii) to identify the precise shape of the response functions (e.g. Pouget 1972; Porter and Gawith 1999; Caffarra et al. 2011a; Baumgarten et al. 2021). However, one needs to note that the experimental approach has also some important limits among which the incomplete representation in controlled conditions of all cues that can affect development and their interactions, and experimental flaws that may lead to unmeasured covariation among treatments that can result in incorrect conclusions (Buonaiuto et al. 2023).

14.3.2 The Numerical Approach

In the numerical approach, field or experimental observations of the timing of phenological events are related to meteorological data gathered at the same location before the event. Phenological observations used to develop and test phenology models have two main origins: historical observations in wild populations or phenological gardens and experimental results. The accompanying meteorological data comes from different sources: loggers on site, weather stations of national meteorological services some distance away, gridded meteorological products.

The numerical approach includes two aspects: the integration of the system of Ordinary Differential Equations (ODEs) i.e. rate equations (Eq. 14.2) for each phase (Fig. 14.1), and the inferring optimal parameters values by minimizing the deviance between the model and observation or maximizing the explained variance. Numerical integration in phenology models often uses a fixed time-step of 1 day or 1 h, i.e. forward Euler integration (Press et al. 1989). The Euler method can have large numerical errors e.g. if the rates of change of the ODEs differ very much. That is the case in the parallel model when the rate of forcing changes very little compared to the rate chilling. The Euler method also has large errors if the ODE changes very rapidly, e.g. such as in Fig. 14.2 around the minimum and maximum temperature of the response functions. Predictor-corrector methods such as Runga-Kutta (Langtangen 2014) aim to reduce this type of numerical error.

Considering finding parameter values by optimizing a goodness of fit metric, multiple goodness-of-fit metrics exist (Willmott 1981, 1982; Gauch et al. 2003; Robeson and Willmott 2023) and many numerical approaches to optimize these. These optimization methods are not equally performant in the case of phenology models. Traditional optimization algorithms such as Downhill Simplex or Newton methods (Press et al. 1989) rarely converge towards the global optimum if there is the strong interdependency of phenological model parameters (Kramer 1994b). The simulated annealing method is more effective in this respect (Chuine et al. 1998, 1999) because it is especially designed for functions with multiple optima. However, which method to use also depends on the quality of the data, so that several optimization methods are tested to reach solid conclusions (Kramer et al. 2017).

More recently Bayesian approaches have also been used to parameterize phenological models. Bayesian approaches coupled with experimental approaches that provide prior information on the distribution of model parameters can be powerful (Dose and Menzel 2004; Thorsen and Hoglind 2010; Fu et al. 2012). Other algorithms such as CMA-ES (REFs) are particularly efficient to fit models with a large number of parameters, but can be less efficient to fit models with fewer numbers of parameters (Meier and Bigler 2023).

Despite the efficiency of those algorithms, critical expert knowledge is often needed to assert the most realistic parameter values obtained when multiple fittings are executed to account for the stochasticity inherent to most non-Bayesian algorithms. Firstly, some parameters may be highly correlated (e.g. the base temperature of a GDD and the critical sum to reach S*), which may lead to several sets of parameters that are statistically equivalent but have very different individual values. Secondly, the estimation of the parameters depends on the data used to adjust the parameters, which represent only a subset of the climatic conditions encountered by the species or variety in its range (the data collected rarely covers the entire geographical area) and/or its lifetime (long-term data series rarely exceed 20 years, which is very short compared with the life expectancy of a tree). This can lead to biased parameter estimates which can become particularly problematic when using models to provide forecasts under future climate conditions (Lobo 2016). Parker et al. (2013) explored the minimum number of observations that should be used to define a robust parameter value: for a GDD-type function the number should be around 20 data from at least three to five sites with contrasting climatic conditions. Below these criteria, the robustness of the parameters obtained is low, and beyond that, it improves very little. Thirdly, some model parameter estimates might differ across a species range due to local adaptation and genetic differentiation (Chuine et al. 2000), and might even be phenotypically plastic (Kramer et al. 2017). This needs to be taken into account in the parameter estimation scheme whenever possible. Because of these shortcomings, it is strongly recommended not to rely solely on goodness-of-fit statistics to select parameter sets, but also on the form of the response functions obtained, which must be realistic, i.e. consistent with what is known from the experimental approach. Finally, Wallach et al. (2023) have recently proposed a simple method to calibrate phenology models in order to avoid overparameterization and help to decrease the prediction error.

14.3.3 A Way Forward

The numerical approach and the experimental approach have both advantages and drawbacks. On one hand, the experimental approach is time consuming and experimental conditions do not always reproduce very well the natural conditions and are always simplified compared to natural conditions where several factors interact with each other. On the other hand, the numerical approach is much quicker, provided that sufficiently long phenological and temperature records are available, and that adequate numerical methods are used, but it does not guarantee the realism of the model and the parameter values, in the sense that the actually operating mechanisms are identified. For example, numerical methods might indicate that photoperiod does not play an important role in explaining the variability in leaf unfolding even when it is experimentally known that photoperiod is an environmental cue for the species (Kramer 1994b). This is typically the case if the variability of photoperiod in the data is small relative to the variability in temperature. Moreover, in observational time series the photoperiod is often correlated with temperature. A combination of both approaches is needed to get realistic and efficient models that will be able to project plant phenology in new climatic conditions.

14.4 Applications of Plant Phenology Models

Plant phenology models are important tools in a wide range of applications such as (1) prediction of the impact of global warming on the phenology of wild and cultivated species (Hänninen et al. 2007; Morin et al. 2009; Hanninen and Tanino 2011); (2) improvement of primary productivity models or crop models (Kramer and Mohren 1996; Krinner et al. 2005; Kramer and Hänninen 2009; Beaudoin et al. 2023); (3) prediction of the occurrence of pollen in the atmosphere, and thus the occurrence of pollen allergies (Frenguelli and Bricchi 1998; Chuine and Belmonte 2004; Garcia-Mozo et al. 2007, 2008a, b); (4) species distribution modeling (Chuine and Beaubien 2001; Morin et al. 2007, 2008); and (5) climate reconstruction using historical phenological data (Chuine et al. 2004; Menzel 2005; Meier et al. 2007; García de Cortázar-Atauri et al. 2010; Maurer et al. 2011; Yiou et al. 2012). In the following paragraphs we describe some of these uses.

14.4.1 Frost Hardiness Modeling

Climate change is increasing the risk of false spring events because of earlier flowering or leaf unfolding dates that expose leaves and flowers to higher risk of exposure to freezing temperatures (Vitasse et al. 2018; Vautard et al. 2023). It is thus necessary to better understand the interaction between endodormancy, ecodormancy, and hardening in order to represent those processes accurately in mechanistic models able to project what will be the risk of exposure to frost in the upcoming decades (Sgubin et al. 2018).

Bud frost hardiness is intimately related to its state of development (Vitasse et al. 2014). Frost hardiness gradually increases while dormancy sets-in and is gradually lost during ecodormancy once endodormancy is broken (Sakai and Larcher 1987). Phenology models of leaf unfolding and flowering have been frequently used to assess the risk of frost damage in perennial plants (Cannell 1985; Cannell and Smith 1986; Hänninen 1991; Kramer 1994a; Murray et al. 1989; Linkosalo et al. 2000). The risk of frost damage can be assessed by estimating minimum air temperatures around budburst (Cannell 1985; Murray et al. 1989; Hänninen 1991; Vitasse et al. 2018). More mechanistic models of cold hardiness have been developed that simulate frost damage over the whole year, and not only around budburst (Kobayashi and Fuchigami 1983b; Repo et al. 1990; Kellomäki et al. 1995; Leinonen et al. 1995). Leinonen (1996) first proposed a frost hardiness model based on bud development state. In Leinonen's (1996) model the state of hardiness is regulated by daily air temperature and photoperiod, and the frost hardiness response to these environmental factors depends on the current state of ontogenic development of the bud. The minimum temperature that can be withstood without damage therefore varies during the annual cycle.

It has been known for a long time that frost hardiness is also dependent on water and soluble sugar contents (Siminovitch et al. 1953). However, this is only recently that the relationships between frost hardiness, carbohydrates contents, bud development states, and environmental cues (temperature and photoperiod) have been incorporated into mechanistic models to predict more accurately frost hardiness (Poirier et al. 2010; Charrier et al. 2013, 2018a, b; Deslauriers et al. 2021).

14.4.2 Forest Growth and Distribution

An important application of phenology models is their contribution to more complex models of forest growth and tree species distribution to assess climate change impacts. The model FORGRO uses phenology and frost hardiness models to simulate tree growth and productivity (Kramer 1995; Kramer et al. 1996; Leinonen and Kramer 2002; Kramer and Hänninen 2009). The onset and end of the growing season can be observed either by recording the changes of the canopy such as budburst, autumn coloration, or loss of foliage, or by measuring gas exchanges between the vegetation and the atmosphere. Both can be tested in a model that couples growth and ontogenetic development. FORGRO describes the effects of CO_2 and temperature on photosynthesis, and the effect of temperature on both plant and soil respiration. The description of these processes can be found in Mohren (1987) and Kramer et al. (1996). Temperature also affects the duration of the growing season and the level of frost hardiness, which can be described using the mechanistic phenological modeling approach presented above in Eqs. 14.1 and 14.2.

Phenology models have also played an important role in plant species distribution prediction in the last twenty years. and played a similar role in insect population dynamics and distribution modeling (see also Chap. 15 in this volume). The model PHENOFIT estimates survival and reproductive success based on the match between annual plant development and local seasonal variations of climate. A mismatch between the two may result in frost injury to flowers and leaves, but also in drought injury should the vegetation period occur during the drought season, or in low fecundity should the period between flowering and fall be too short or too cold for fruit to mature (Pigott and Huntley 1981). These mismatches decrease primary productivity, survival and reproductive success. Using PHENOFIT, Chuine and Beaubien (2001) showed that phenology was a major determinant of species range. More precisely, they showed that phenology partly drives southern boundaries because of the inability to fully develop leaves and flowers due to insufficient chilling to break endodormancy, and also drives northern range limits due to a too-short growing season length preventing fruit to reach maturation.

14.4.3 Modeling the Adaptive Response of Phenological Traits to Climate Change

The seasonal coordination of phenology to local climate conditions has several major impacts on plant survival and reproduction (fitness), as well as on competitive relationships *via* vegetative and reproductive performances (Lechowicz and Koike 1995; Chuine 2010). A recent development in phenology modeling is thus to assess the adaptive response of traits, such as the critical state of chilling in response to climate change and the corresponding effect on the budburst to temperature. This approach was first described in Kramer et al. (2008) and applied to the northern limits of *Fagus sylvatica* L. (Kramer et al. 2010). The results indicate that adaptation of the timing of budburst in trees is likely to occur even if the rate of climate change occurs in a time span similar to the longevity of individual trees. Moreover, specific forest management may increase the rate at which the timing of budburst adapts to climate change. The theoretical background in this type of process-based genetic modeling is presented in Kramer and Van der Werf (2010) and Berzaghi et al. (2020).

Using the model PHENOFIT, Duputié et al. (2015) also showed that the plasticity of the date of budburst will help tree species to adapt to global warming, but to a certain extent only. Some species, such as Scots pine, which have been planted widely outside the border of their original climatic niche, are at the limit of the plasticity of the budburst date, which will not help sustaining future climatic conditions in southwestern Europe (Duputié et al. 2015). Finally, the ability to link mechanistically phenological events to environmental conditions on one hand and to fitness on the other hand, also allows investigating the selective pressures imposed by climate and global warming on phenological events (Gaüzere et al. 2020).

14.4.4 Climate Reconstruction Using Historical Phenological Data

Phenology observations are a very good proxy for past climate reconstructions (Brazdil et al. 2005). Both correlative (Aono and Omoto 1993; Menzel 2005; Meier et al. 2007; Etien et al. 2008, 2009; Maurer et al. 2009, 2011; Aono and Saito 2010; Možný et al. 2010); and mechanistic phenology models have been used in this task (Chuine et al. 2004; García de Cortázar-Atauri et al. 2010; Yiou et al. 2012). The latter approach, in particular, made use of grapevine harvest dates to reconstruct temperature anomalies over the last seven centuries (Fig. 14.3, Chuine et al. 2004), as well as atmospheric pressure anomalies over the last five centuries based on temperature gradients (Yiou et al. 2012). Garcia de Cortazar-Atauri et al. (2010) however warned of the difficulties of such reconstructions. They require robust phenological models parameterized with large data series as well as a good knowledge of the history and denomination of grape varieties, historical events such as wars that can affect harvest dates independently of climate, and of historical changes in agricultural practices that may have affected grape harvest dates.

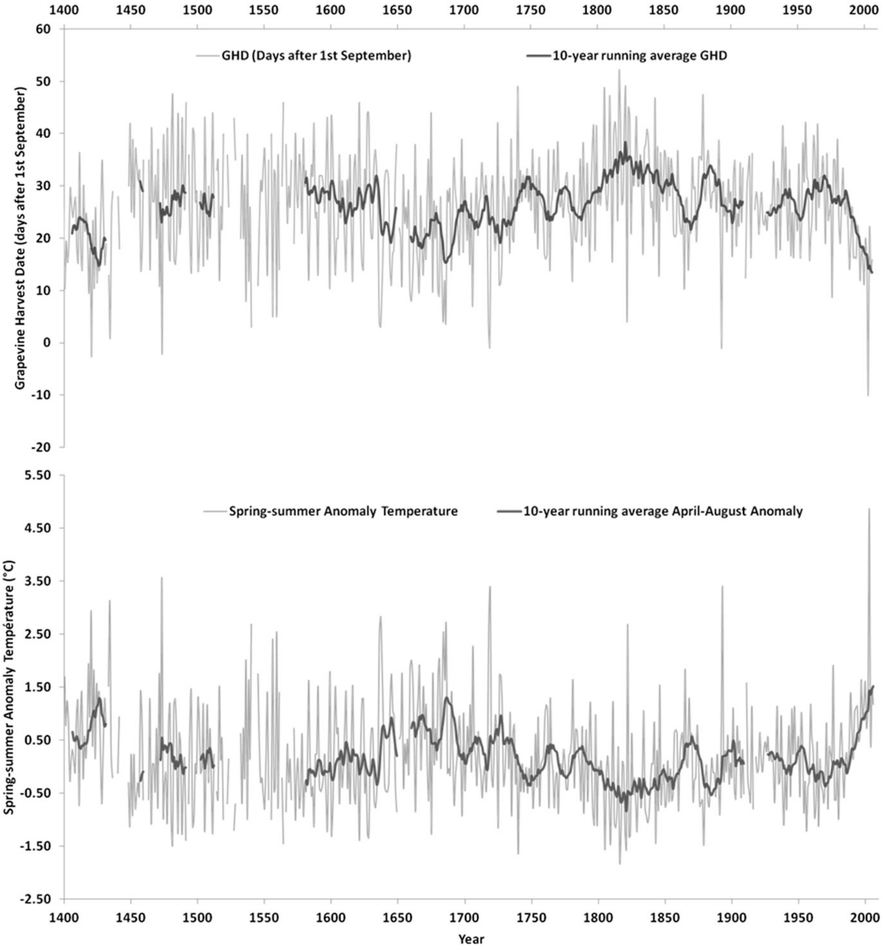

Fig. 14.3 Grapevine harvest date evolution (days after September 1st) in Burgundy (**a**). Reconstructed temperature anomalies of mid-March to August temperature deduced from grapevine harvest dates in Burgundy (**b**). Bold lines: 10-year running average. (Reproduced with permission from Chuine et al. 2013)

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