Chapter 15 Plant Development Models

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Abstract In this chapter we provide a brief overview of plant phenology modeling, focusing on mechanistic phenological models. After a brief history of plant phenology modeling, we present the different models which have been described in the literature so far 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 phenological models have been successfully used for, such as frost hardiness modeling, tree growth modeling, tree species distribution modeling and temperature reconstruction of the last millennium.

15.1 An Overview of Phenology Modeling During the Last Three Centuries

Phenology modeling has a long history starting in 1735 with a publication by de Reaumur (1735). Reaumur 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.

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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. Global warming is expected to have major impacts on plant functions and fitness, as increasing temperatures change the timing of phenological events (Cleland et al. 2007; Chuine 2010).

Most of plant phenology modeling studies have focused on leaf unfolding and flowering, and much fewer on fruit maturation, growth cessation or leaf senescence. This is in part due to the fact that leaf unfolding and flowering are the most widely observed phenophases, and the timing of these events can be observed accurately. This is much less the case for fruit maturation and leaf coloration. In addition, leaf unfolding is very important for primary production (Piao et al. 2007; Richardson et al. 2010) and flowering largely determines plant reproductive success (see Sect. 15.4).

Most phenology models were developed for tree species, rather than non-woody species (Table 15.1). Many more phenological modeling studies focus on temperate biota than on boreal, tropical or sub-tropical biota (Kupias and Mäkinen 1980; Phillipp et al. 1990; Reich 1994; Thorhallsdottir 1998).

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 consequently often comes from different sources. In the case of phenological observations in gardens or experiments, accurate meteorological observations are often made on site. In the case of phenological observations on wild populations, meteorological data are usually obtained from weather stations some distance away. Both data types are useful for phenology modeling, but imply different methodologies as we discuss in Sect. 15.3.

15.2 An Overview of Plant Phenology Models

Reaumur (1735) first introduced the concept of degree-day summation, i.e. daily average temperatures accumulated between an arbitrary date of onset and the date of an observed phenological event. Reaumur found that a lower sum of degree-days was accumulated in April, May and June in 1735, when harvesting of crop and grapes took place late, than in 1734 when the harvest took place early. He realized that a plant develops quicker at a higher temperature, thus shortening the interval between sowing and crop harvest, or flowering and vine harvest. He proposed that plant development is proportional to the sum of temperature over time rather than to temperature during the phenological event itself. In many studies since Reaumur, accumulated temperature is recognized as the main factor influencing year-to-year variation in phenology. Three main types of phenology models exist: analytical, statistical, and mechanistic. Analytical models are based on the cost/benefit tradeoff of producing leaves to optimize resource acquisition (Kikuzawa 1991, 1995a, b, 1996; Kikuzawa and Kudo 1995) and

Table 15.1 List of the different phenological models described in the literature (EcoD, ecodormancy; EndoD, endodormancy, DI, dormancy induction)

Model name	Phenophase	Plant types	Reference
Growing degree hours	EcoD	Fruit trees	Anderson et al. (1986)
Chilling hour	EndoD	Fruit trees	Bennett (1949) and Weinberger (1950)
Bidabé	EndoD + EcoD	Apple tree	Bidabé (1967)
Smoothed Utah	EndoD	Fruit trees	Bonhomme et al. (2010)
Dormphot	DI, EndoD, EcoD	Forest trees	Caffarra et al. (2011)
Alternating	EndoD + EcoD	Forest trees	Cannell and Smith (1983) and Kramer (1994b)
Unified	EndoD + EcoD	Trees	Chuine (2000)
Unichill, Uniforc	EndoD + EcoD	Trees	Chuine et al. (1999)
Growing degree-days	EncoD	Crops, grapevine	de Reaumur (1735) in Wang (1960)
Delpierre	Senescence	Forest trees	Delpierre et al. (2009)
Dynamic model	EndoD	Fruit trees	Erez et al. (1990) and Fishman et al. (1987)
Hartkamp	EcoD	Velvet bean	Hartkamp et al. (2002)
Triangle GDH	EcoD	Crops	Hammer et al. (1993)
Sequential	EndoD + EcoD	Forest trees	Richardson et al. (1974) and Hänninen (1987)
Hänninen	EndoD + EcoD	Forest trees	Hänninen (1990) and Hänninen (1995)
Biological days	EcoD + EndoD	Crops	Hunt and Pararajasingham (1995)
Kobayashi and Fuchigami	EcoD	Red osier dogwood	Kobayashi and Fuchigami (1983a)
Deepening rest	EndoD + EcoD	Red osier dogwood	Kobayashi et al. (1982)
Kramer	EndoD + EcoD	Forest trees	Kramer (1994b)
Parallel	EndoD + EcoD	Forest trees	Hänninen (1987) and Landsberg (1974)
Promoting inhibition model	EndoD + EcoD	Fruit trees	Linkosalo et al. (2008)
Positive Utah	EndoD	Fruit trees	Linsley-Noakes et al. (1995)
Logarithmic (Action days)	EcoD	Grapevine	Pouget (1968)
Utah + GDH	EndoD + EcoD	Fruit trees	Richardson et al. (1974)
Asymcur	EndoD	Fruit trees	Richardson et al. (1982)
Sinusoidal-parabolic GDH	EcoD	Grapevine	Riou (1994)
Robertson	EcoD	Crops	Robertson (1968)
Sinclair	EcoD	Crops	Sinclair et al. (1991)
Soltani	EcoD	Chickpea	Soltani et al. (2006)
Four phase	EndoD + EcoD	Trees	Hänninen (1990) and Vegis (1964)
Asymetric unimodal function	Flowering and fruit maturation	Wheat	Wang and Engel (1998)
White	Senescence	Land surface	White et al. (1997)

(continued)

Model name	Phenophase	Plant types	Reference
Asymetric unimodal		Annual crops	Yan and Hunt (1999)
function	maturation		
Asymetric unimodal	Flowering and fruit	Annual crops	Yin et al. (1995)
function	maturation		

are designed to understand the evolution of leaf lifespan strategies in trees, rather than the annual variation in plant phenology.

Statistical phenology models relate the timing of phenological events to climatic factors. Their parameters are estimated from data using various statistical fitting methods. While most of these models do not consider specific biological processes, some are more mechanistic than others. Some are 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). Others are more complex. For example, the Spring Indices Models (Schwartz and Marotz 1986, 1988; Schwartz 1997; Schwartz et al. 2012) have been successfully used to predict the start of the growing season in North America. It is a multiple regression model of the type:

$$y^{-1} = C + \sum_{k=1}^{n} A_k X_k \tag{15.1}$$

where y is the day-of-the-year date of the phenological event, C and A_k are constants and X_k are the predictor variables, degree-day sums for two threshold temperatures (-0.6 or 5 °C), mean temperature, and number of synoptic weather events (in particular warm air advection).

Mechanistic models formally describe known or hypothetical cause-effect relationships between physiological processes and some driving factors in the plant's environment. New relationships should be introduced in a mechanistic model only if information on their impacts on the process is available. It is important to note that parameters of mechanistic models have physical dimensions that can, in principle (see Sect. 15.3), be measured directly instead of being estimated by fitting. However, this is rarely possible in plant phenology models. As most models described in the literature are of this type, the following paragraphs provide a detailed overview of their hypotheses. The structure of mechanistic models is usually based on systems theory rather than statistical inference (Hänninen and Kramer 2007; Chuine 2010).

From experimental evidence we know at least three things. First, higher temperature accelerates cell growth during ecodormancy, during which dormancy is caused by external factors (Lamb 1948; Sarvas 1972, 1974; Landsberg 1974; Campbell and Sugano 1975; Lang et al. 1985; Caffarra et al. 2011b). Second, endodormancy, during which dormancy is caused by internal factors (Lang et al. 1985) must be broken by a chilling period at cool temperatures before plants enter

the phase of ecodormancy (Sarvas 1974; Hänninen 1990; Caffarra et al. 2011a). Third, the evidence for the role of photoperiod in tree phenology is conflicting, depending on phenophase (a plant's phenological state), species and location (Heide 1993a, b; Kramer 1994b; Falusi and Calamassi 1996). However, there is clear evidence that long photoperiod enhances cell growth, compensating for a lack of chilling during the endodormancy phase (Wareing 1953; Heide 1993b; Myking and Heide 1995; Caffarra et al. 2011a).

Most differences between mechanistic phenological models come from the number of different phases they consider and the response function to temperature or photoperiod they consider for each phase. The general structure of mechanistic phenological models is the following:

$$t_n$$
 such that $S_{n,t} = \sum_{t_{n-1}}^{t_n} R_{n,t}(Z) = S_n^*$ (15.2)

where n is a development phase (e.g., encodormancy, 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 phenological 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:

$$R_{1,t}(x_t) = \begin{cases} 0 & \text{if } x_t \le T_b \\ x_t - T_b & \text{if } x_t > T_b \end{cases}$$
 (15.3)

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 .

For tree species, more complex models take into account the endodormancy and dormancy inductions phases. Two-phase models for leaf unfolding and flowering typically take endodormancy into account in addition to ecodormancy (e.g., the Sequential, Parallel, Alternating, Deepening Rest models). Three-phase models for leaf unfolding or flowering typically describe the dormancy induction phase in addition to endodormancy and ecodormancy phases (Dormphot model). The Fourphase 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.

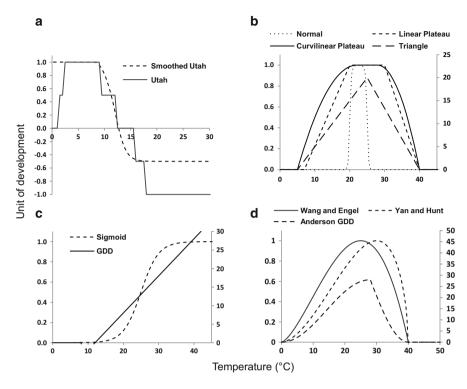


Fig. 15.1 Examples of response to temperature during dormancy induction, endodormancy and ecodormancy. (a) Utah and smoothed Utah response functions; (b) normal, triangular, linear plateau and curvilinear plateau response functions; (c) sigmoid and growing degree-day response functions; (d) Wang and Engel, Yan and Hunt and Anderson response functions (see Table 15.1 for the references)

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, a 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 depending on phase (Fig. 15.1).

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. Hänninen (1990, 1995) introduced a unifying formulation for several model types. In this approach, temperature responses of the sub-models are fixed *a priori*. Kramer (1994a, b) broadened the approach with a fitting procedure to select between different forms of the three sub-models (see Hänninen and Kramer 2007 for a review). Chuine (2000) further generalized model formulation with a Unified model that is based on two general functions to describe

the relationships between rates of development and temperature during endodormancy (Fig. 15.1b) and ecodormancy (15.1c). The Unified model is flexible and includes as a special case basically any phenological model where air temperature is the driving factor.

To facilitate the development and the parameterization of mechanistic phenological models, a software package called PMP (Phenology Modeling Platform) has been designed and can be downloaded freely from (http://www.cefe.cnrs.fr/en/logiciels/ressources-documentaires). PMP can be used to parameterize a phenological model using meteorological data and phenological observations, or to run simulations using an available phenological model and meteorological data. The user can parameterize existing models chosen from a library, create a new model from scratch or build from on an existing one. The construction of the model requires determining the number of phases to be considered and for each phase, which meteorological variables have an impact and which response function should be used. The action of a meteorological variable can impact the effect of another variable within a phase, and phases can follow each other either sequentially or in parallel (influencing each other). Model parameter estimates are jointly optimized using the simulated annealing algorithm of Metropolis (Chuine et al. 1998) [see Sect. 15.3.2], and confidence intervals for parameters can be calculated.

15.3 Methodological Considerations

The critical problem with mechanistic phenology models is that the basic biochemistry and biophysics of certain phases is sometimes incompletely understood. This is especially true of the dormancy phase. Therefore, we cannot make direct measurements of model parameter values. Two approaches are used to estimate these values: the experimental approach, that analyzes the temperature response of growth and development under controlled conditions; and the numerical approach, that uses statistical model-fitting techniques.

15.3.1 The Experimental Approach

The experimental approach consists of experiments carried out to analyze the underlying mechanisms of phenological responses, one mechanism at a time. A few studies have followed this method.

Sarvas (1972) determined experimentally the temperature response of development rate during ecodormancy, using observations of meiosis in pollen mother-cells of several forest tree species. He noticed that *developmental time*, i.e. the average time between two meiotic phases declines exponentially with increasing temperature. Thus, the *rate of development* (i.e., the reciprocal of development time) increases with temperature is a sigmoid fashion. He tested this model with the

timing of flowering in forest stands. Although the Thermal Time model with a +5 °C threshold temperature approximates quite well the temperature response measured in the laboratory, Sarvas (1972) also found that ontogenetic development could take place between -3 and +5 °C. As the physiological processes of dormancy release were unknown, and still are, Sarvas (1974) 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. 15.1b).

Experimental studies also allow the identification of critical temperatures for growth and development of many species and their differences between cultivars (in crops), for example wheat (Porter and Gawith 1999) or grapevines (Pouget 1972), or between provenances (in forest trees).

An experimental approach was also used by Hänninen (1990), who developed the first version of the Unified model to compare various model assumptions concerning the effects of chilling on the response of buds to forcing temperatures. In seedling of *Pinus sylvestris* and *Picea abies*, he found that the effects fell somewhere between the assumptions of the Sequential and the Parallel models.

The Dormphot model of Caffarra et al. (2011a) is also the outcome of experimental results on beech. An interaction between photoperiod and temperature was found during ecodormancy, when longer photoperiod decreases the optimal temperature of development and accelerates bud growth (Caffarra et al. 2011b). These experiments also showed that the accelerating action of photoperiod decreased as the amount of chilling increases.

15.3.2 The Numerical Approach

The statistical approach estimates parameter values with statistical model-fitting techniques. In this approach, field or experimental observations of the timing of phenological events are related to meteorological data gathered at the same location before the event. Two techniques have been used, both estimating parameters using the least squared residuals method.

The easiest method is to fix all but one parameter to a given value, and find the value of the free parameter that minimized the sum of squared residuals. All parameters are varied this way one after the other. This technique has several limits, most importantly (i) a finite number of parameter values can be tested, (ii) parameter values are estimated independently from each other although they are usually not independent, (iii) the least squares function may have several local optima and it is almost impossible to find the global optimum without a more thorough search.

More efficient methods consist in estimating all parameters simultaneously using optimization algorithms. Traditional optimization algorithms such as Downhill

Simplex or Newton methods (Press et al. 1989) rarely converge towards the global optimum because of 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. 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).

However, accurate parameter estimation is not sufficient, prediction accuracy is also critical, because phenology models must 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). 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 case, one can resort to "leave one out" (or jackknife) cross-validation (Stone 1977; Häkkinen 1999).

The above discussion shows that parameter estimates of phenology models can be developed with two quite different approaches. The experimental approach uses detailed ecophysiological laboratory or greenhouse experiments. This is a time-consuming process. Because model parameters may be under genetic control, they often need to be measured for different populations. The statistical approach is much quicker, provided that sufficiently long phenological and temperature records are available, and that adequate statistical methods are used. However, this may be too rough an approach and a combination of the two (experimental and statistical) is probably the best solution to obtain accurate and realistic models.

15.4 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 (Kramer and Mohren 1996; Krinner et al. 2005; Kramer and Hänninen 2009), (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. 2004b; 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.

15.4.1 Frost Hardiness Modeling

Phenology models of bud burst have frequently applied to assess the risk of frost damage to perennial plants (Cannell 1985; Cannell and Smith 1986; Murray et al. 1989; Hänninen 1991; Kramer 1994a; Linkosalo et al. 2000). Bud development and growth is highly correlated to loss of frost hardiness (Sakai and Larcher 1987). Frost hardiness gradually increases while dormancy sets-in and is gradually lost during ecodormancy once endodormancy is broken. The risk of frost damage can be assessed by estimating minimum air temperatures around bud burst (Cannell 1985; Murray et al. 1989; Hänninen 1991). More mechanistic models of cold hardiness have been developed that simulate frost damage over the whole year, and not only around bud burst (Kobayashi and Fuchigami 1983b; Repo et al. 1990; Kellomäki et al. 1995; Leinonen et al. 1995). Leinonen (1996) developed the most complex and probably most accurate frost hardiness model so far. In this 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. The minimum temperature that can be withstood without damage varies during the annual cycle. Leinonen introduced an injury that responds to temperature according to the current frost hardiness. It has been known for a long time that frost hardiness is also dependent on water and soluble sugar contents (Siminovitch et al. 1953). Recent studies have tried to model this relationship mechanistically (Poirier et al. 2010).

15.4.2 Forest Growth and Climate Change

An important application of phenology models is their coupling with general models of forest growth to assess climate change impacts. 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 bud burst, autumn coloration or loss of foliage, or by measuring gas exchanges between the vegetation and the atmosphere. Part of the springtime CO₂ flux is caused by the activity of the understory, which is not described by the FORGRO model (Vesala et al. 1998). The decline of the CO₂ exchange from mid-summer to autumn is mainly the direct effect of decreasing light availability and temperature on photosynthesis (Vesala et al. 1998). A rise in atmospheric CO₂ concentration and temperature influences a multitude of processes in a tree and in a forest stand. FORGRO describes the direct effects of CO2 and temperature on photosynthesis, and the direct effect of temperature on both plant and soil respiration. The description of these processes can be found in Kramer et al. (1996) and Mohren (1987). Indirect effects of temperature include the duration of the growing season and the level of frost hardiness.

15.4.3 Modeling the Adaptive Response of Phenological Traits to Climate Change, and Species Niche

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 phenological modeling is to assess the adaptive response (in a genetic sense) of traits such as chilling requirement to climate change, and its consequence on the effect of temperature on the timing of budburst. This approach is 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 bud burst adapts to climate change. The theoretical background in this type of process-based genetic modeling is presented in Kramer and Van der Werf (2010).

Phenological models have also played an important role in species distribution prediction in the last 10 years. Using a species range model (Phenofit) Chuine and Beaubien (2001) showed that phenology was a major determinant of species range. 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.

Phenofit has been validated for 22 tree species from North America and Europe (Morin et al. 2007; Gritti et al. 2013) and has been used to predict species distribution changes under different climate scenarios (Morin et al. 2008). Sensitivity analysis showed that the southern boundaries of many species were determined by the inability to fully develop leaves or flowers due to insufficient chilling to break endodormancy, while northern range limits were usually due to the inability to ripen fruit. Western and eastern range limits are usually more sensitive to the ability of the species to resist water stress. Phenological models have played a similar role in insect population dynamics modeling and more recently insect distribution modeling (see Chap. 16).

15.4.4 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 phenological models have been

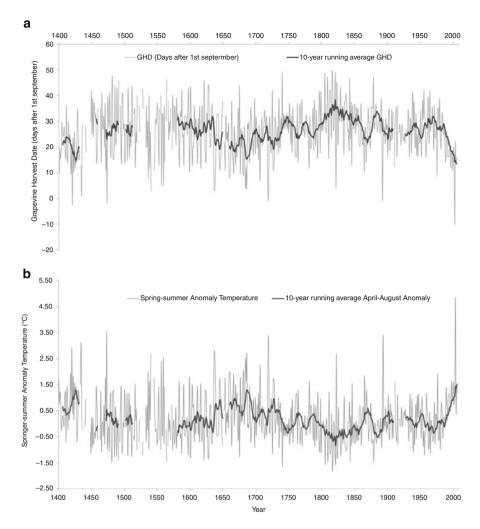


Fig. 15.2 Grapevine harvest date evolution (days after September 1st) in Burgundy (a). Reconstructed temperature anomalies of mid-March to August temperature deduced from grapevine harvest dates in Burgundy (b). *Bold lines*: 10-year running average

used in this task (Chuine et al. 2004a; 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. 15.2, Chuine et al. 2004), as well as atmospheric pressure anomalies over the last five centuries based on temperature gradients (Yiou et al. 2012). García de Cortázar-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 impacted on grape harvest dates.

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