

# Plant phenological modeling and its application in global climate change research: overview and future challenges

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**Abstract:** Plants interact to the seasonality of their environments, and changes in plant phenology have long been regarded as sensitive indicators of climatic change. Plant phenology modeling has been shown to be the simplest and most useful tool to assess phenol–climate shifts. Temperature, solar radiation, and water availability are assumed to be the key factors that control plant phenology. Statistical, mechanistic, and theoretical approaches have often been used for the parameterization of plant phenology models. The statistical approaches correlate the timing of phenological events to environmental factors or heat unit accumulations. The approaches have the simplified calculation procedures, correct phenological mechanism assumptions, but limited applications and predictive abilities. The mechanistic approaches describe plant phenology with the known or assumed “cause–effect relationships” between biological processes and key driving variables. The mechanistic approaches have the improved parameter processes, realistic assumptions, broad applications, and effective predictions. The theoretical approaches assume cost–benefit tradeoff strategies in trees. These methods are capable of capturing and quantifying the potential impacts and consequences of global climate change and human activity. However, certain limitations still exist related to our understanding of phenological mechanisms in relation to (1) interactions between plants and their specific climates, (2) the integration of both field observational and remote sensing data with plant phenology models across taxa and ecosystem type, (3) amplitude clarification of scale-related sensitivity to global climate change, and (4) improvements in parameterization processes and the overall reduction of modeling uncertainties to forecast impacts of future climate change on plant phenological dynamics. To improve our capacity in the prediction of the amplitude of plant phenological responses with regard to both structural and functional sensitivity to future global climate change, it is important to refine modeling methodologies by applying long-term and large-scale observational data. It is equally important to consider other less used but critical factors (such as heredity, pests, and anthropogenic drivers), apply advanced model parameterization and data assimilation techniques, incorporate process-based plant phenology models as a dynamic component into global vegetation dynamic models, and test plant phenology models against long-term ground observations and high-resolution satellite data across different spatial and temporal scales.

**Key words:** plant phenology, climate change, NDVI, ecological forecasting, process-based model.

**Résumé :** Les plantes interagissent avec la saisonnalité de leur environnement et on a longtemps considéré les changements de la phénologie comme indicateurs du changement climatique. On a montré que la modélisation de la phénologie des plantes constitue le moyen le plus simple et le plus utile pour évaluer les glissements phéno–climatiques. On assume que la température, la radiation solaire et la disponibilité de l'eau constituent des facteurs déterminants contrôlant la phénologie des plantes. On a également souvent utilisé des approches statistiques, mécanistes et théoriques pour paramétrer les modèles de phénologie végétale. Les approches statistiques font la corrélation entre l'incidence des événements phénologiques, les facteurs environnementaux ou les accumulations d'unités thermiques. Ces approches statistiques ont l'avantage d'utiliser des méthodes de calcul simplifiées et de corriger les mécanismes phénologiques assumés mais ont des capacités d'application et de prédiction limitées. Les approches mécanistes décrivent la phénologie des plantes avec les relations de causes à effets connues ou présumées impliquant les processus biologiques et des variables déterminantes. Les approches mécanistes ont l'avantage d'améliorer le paramétrage des processus, d'établir des postulats réalistes et de fournir des applications et des prédictions valables. L'approche théorique se base sur des stratégies coût bénéfice dans l'arbre. Ces méthodes peuvent intégrer et quantifier les impacts potentiels et les conséquences du changement climatique global et de l'activité humaine. Cependant, il existe toujours certaines limitations liées à notre compréhension des mécanismes phénologiques en relation avec (1) les interactions entre les plantes et les climats spécifiques, (2) l'intégration à la fois des données de terrain et de télédétection avec les modèles phénologiques végétaux à travers les taxons et les types d'écosystèmes, (3) la clarification de l'amplitude et de la sensibilité liées à l'échelle du changement climatique global et (4) l'amélioration des processus de paramétrisation et la réduction générale des incertitudes de la modélisation pour prédire les impacts du changement climatique futur sur la dynamique phénologique des plantes. Pour améliorer notre capacité à prédire l'amplitude des réactions phénologique des plantes en relation avec la sensibilité à la fois structurale et fonctionnelle du futur changement climatique, il faut raffiner les méthodologies de modélisation en appliquant des données à long terme et à grande échelle. Il faut également considérer des facteurs moins utilisés mais critiques (comme l'hérédité, les pestes et les déterminants anthropiques), appliquer la paramétrisation de modèles avancés et des techniques d'assimilation des données, incorporer des modèles de phénologie végétale basés sur des processus comme composante dynamique des modèles

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globaux dynamiques de la végétation et tester les modèles de phénologie végétale contre des observations à long terme ainsi que les données satellites à haute résolution sur différentes échelles spatiales et temporelles. [Traduit par la Rédaction]

**Mots-clés :** phénologie végétale, changement climatique, NDVI, prévisions écologiques, modèle basé sur des processus.

## 1. Introduction

Phenology is the scientific study of periodic plant and animal life cycle events (such as flowering, breeding, and migration) and how these are influenced by seasonal and interannual variations in climate. Phenological records of the dates on which seasonal phenomena occur can provide important information on how climate change affects ecosystems over time. Plants serve a number of vital functions within the biosphere throughout all possible spatial scales. Studies related to plants could be addressed at spatial scales of species distribution (e.g., range size and its shifts) and at temporal scales from millennia to decades with the shifts of reproduction age, succession stage, and, most importantly, phenology (Thuiller 2007). Plant phenology is generally looked upon as the study of specific temporal aspects of vegetation and the biosphere. It is associated with the timing of plant activities: emergence, growth (early and late vegetative phases), flowering, fructification, senescence, and the root causes in connection with biotic and abiotic drivers as well as interrelations that occur among phases for different species (Lieth 1974).

Seasonal rhythms of plant development have been used for centuries in support of human activity, particularly for agriculture, horticulture, silviculture, and medical service (Hopp 1974). Since plant phenology (here primarily pertaining to tree species) could provide much information on the conditional changes of global climate conditions and the consequent shifts in plant life pulses, recent experimental and simulation efforts demonstrate its current revival in the aid of the urgency of investigations targeted to provide new insights into plant phenology and its relationships with abiotic factors for little-known ecosystems (e.g., Cleland et al. 2007; Forrest et al. 2010; Chambers and Keatley 2010; Ault et al. 2011; Liang et al. 2012). The plant phenology model, the algorithmic realization of the “phenology–climate” connection, has become a crucial tool for ecological and climate researchers to quantify phenological responses to climatic drivers and a way in which to gather potential feedback of phenological shifts caused by climate change (e.g., Cleland et al. 2007; Thackery et al. 2010; van Vliet 2010). Over the last three decades, much of the modeling efforts carried out in relation to plant phenology has been focused on addressing controls on phenology (environmental factors, biological processes, and intrinsic traits; e.g., Schwartz et al. 2006), modeling techniques (statistical, mechanistic, or theoretical approaches; e.g., Kathuroju et al. 2007; Diez et al. 2012), and ecosystem-level and evolutionary consequences of phenological changes (species survival, distribution, energy, and CO<sub>2</sub> flux; e.g., Chuine et al. 2004; Cleland et al. 2007; Morin et al. 2008; van Vliet 2010). In the development of plant phenology in the course of the entire modeling study, there are three trends: from single factor to many factors, from simple to complex, and from small to large scales. They ranged from the one parameter “Degree Day” model (Cannell and Smith 1983) to remote sensing based plant phenology models (e.g., Migliavacca et al. 2008; Peng et al. 2011). To date, no comprehensive literature review exists that summarizes recent developments in plant phenology models. The objectives of this paper are to (1) highlight the importance of plant (primarily trees) phenological research and synthesize the potential effects of key environmental factors on plant phenological processes; (2) summarize recent advances in plant phenology models associated with the study of impacts of global climate change on terrestrial ecosystem structure, functions, and services as well as feedbacks that occur between the biosphere and the atmosphere; and (3) further discuss existing problems and future challenges and perspectives of plant phenology models.

## 2. Factors controlling plant phenology

Plant phenology at species-specific level is the consequence from two opposing factors: an intrinsic or characteristics and an environmental component. The intrinsic traits of plants, or characteristics of an individual plant (e.g., genome, age, and evolution within a plant community), is associated with biotic potential, photosynthetic activity, absorption of nutrients, constructive metabolism, etc. The environmental component is representative of the restraints imposed by competition, limited resources, stress, respiration, and aging factors (e.g., Chuine 2010; Ibáñez et al. 2010) (summarized in Fig. 1).

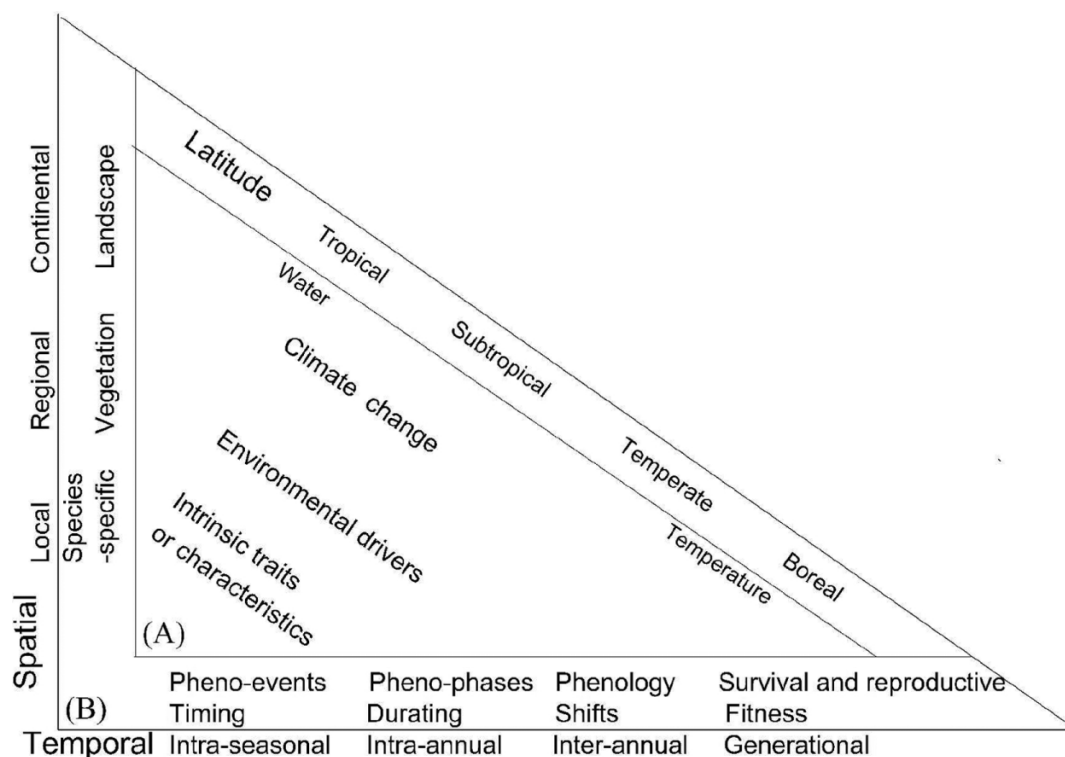
Generally, spatial variations of plant phenology (primarily tree species) are limited by low temperatures at high latitudes and by water deficits inherent in desert and arid regions (e.g., Beaubien and Freeland 2000; Moser et al. 2010; Visser et al. 2010; Wilczek et al. 2010). However, the photoperiodic role of tree phenology largely depends on tree species type and location (mid and high latitudes) (Borchert and Rivera 2001). Regional limitations vary in their degrees of impact on growth throughout the growing season (e.g., Sparks et al. 2000; Miller-Rushing et al. 2007). Key environmental drivers such as solar radiation, temperature, and water availability in their relation to temporal (intraseasonal and interannual) changes in plant phenology have been widely studied (e.g., Kramer et al. 2000; Badeck et al. 2004; Cleland et al. 2007; Forrest et al. 2010; Forrest and Miller-Rushing 2010). Intraseasonal timing of plant phenological events is primarily driven by temperature and photoperiod (e.g., Chmielewski et al. 2004). The daily temperature fluctuation and the number of frost-free days in the given period also seem to be determinant for phenophases (Eppich et al. 2009). It, however, is also important to consider precipitation when studying pollen season, flowering, fruit production, etc. (Galán et al. 2001; Crimmins et al. 2010). Furthermore, soil properties (e.g., soil texture, water availability, nutrients, etc.) affect plant growth. Biological processes (e.g., pests, insects, and competition) also play an important role in the individual development of plant species. Many other local factors that include shading, soil conditions, nutrient concentrations, and pathogens also interact with other key drivers, which could determine physiological responses of plants and their phenology (Winder and Cloern 2010; Ibáñez et al. 2010). Finally, climatic factors and climate patterns that range from intraseasonal to decadal to century scales directly influence the timing, magnitude (productivity), and spatial patterns of vegetation growth cycles, and, for that matter, phenological response (Schwartz 1994).

In turn, the processes of plant phenology, a fundamental characteristic of species and ecosystem dynamics, are likely to affect all components of biodiversity (genes, species, and ecosystems) and the interactions between species. Also, plant phenological changes have many socio-economic consequences and affect millions of people in a wide range of sectors (notably agriculture, fisheries, forestry, and public health). The socio-economic costs of adaptation to plant phenological changes in these sectors are, however, rarely quantified but will be considerable (e.g., Chuine 2010).

## 3. Plant phenology models

Based on our understanding of key parameters that trigger or control changes in plant phenological events, various plant phenology models that boast diverse criteria have been developed and tested with varying degrees of success (see Table A1). In a previous review by Cleland et al. (2007), plant phenology models were divided into species-specific and vegetation-type models. According to the input data, most existent species-specific models focus on

**Fig. 1.** Factors controlling plant phenology. Framework of phenology–climate interactions: (A) inside triangle shows the affecting components and factors to controlling plant phenology as a perspective of study; (B) outside triangle displays the tempo-spatial dimension of plant phenology to address all scale issues related to plant (trees for consideration).



generating separate and separately parameterized model results for each plant species and variety considered. Črepinšek et al. (2006) proposed that the species-specific model should function as a phenological or phenoclimatic model. Marker species were identified by using long-term empirical or statistical observational data of plant phenophases (García-Mozo et al. 2002). Phenoclimatic indicators primarily focus on environmentally driven responses of plant timing traits in light of a wide diversity of physiologically motivated thermal (Sitch et al. 2003), photothermal (White and Nemani 2003), and hydrothermal (Sitch et al. 2003) models developed for various plant species and phenological traits. Häkkinen et al. (1995) defined five categories of plant phenology models in relation to budburst: critical time or day length model, temperature sum model, a model based on respiration, a period unit model, and a model fitted for feedback development. Although the data requirements, design, and output variables of these models may vary according to their purpose as well as their level of focus, they can be categorized into the following three primary classifications (traditionally used to identify different modeling philosophies developed over the last 30 years) (see Fig. 2): statistical, mechanistic, and theoretical (Črepinšek et al. 2006; Cleland et al. 2007) (see Table A1).

### 3.1. Statistical (empirical) approach

At present, the plant physio-ecological process based phenological model lacks in necessary functionality. Statistical based plant phenology models, also called empirical plant phenology models, correlate the timing of phenological events to different environmental factors (primarily climatic) without consideration of specific biological processes. Their parameters are derived from empirical data by various statistical fitting methods. Some of these fitting methods assume simple linear correlations with average temperatures during different periods of the year (Galán et al. 2001). The linear empirical model can be written as  $\hat{y} = \mathbf{X}\mathbf{b}$  with  $\mathbf{b} = (\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'\mathbf{y}$ , where vector

$\mathbf{y}$  contains a set of values observed in the past, the columns of matrix  $\mathbf{X}$  contain simultaneously observed values of relevant predictors together with a column of ones, vector  $\mathbf{y}$  presents the model estimates of observed  $\mathbf{y}$ ,  $\mathbf{b}$  is the vector of regression coefficients estimated on the base of observed  $\mathbf{y}$  and  $\mathbf{X}$ , and  $\mathbf{X}'$  denotes transposed matrix (Krzanowski 1998).

Also, they assume that an event occurs when a certain number of heat units ( $U_t$ ) above a lower threshold or base temperature ( $T_b$ ) have accumulated (McMaster and Wilhelm 1997; Snyder et al. 1999). Others are more complex. These incorporate either a few or numerous input parameters (Schwartz 1999), for example, the photo-heat unit ( $U_{pt}$ ), the hydro-heat unit ( $U_{wt}$ ), and feature multiple linear regressions (Wilks 1995; Storch and Zwiers 1999). Based on these hypotheses, the statistical plant phenology model such as heat sums, degree days, growing degree days, physiological time, thermal time or the Spring Warming model (Cannell and Smith 1983; Hunter and Lechowicz 1992) has been developed (see Table A1). The heat unit model can be written as

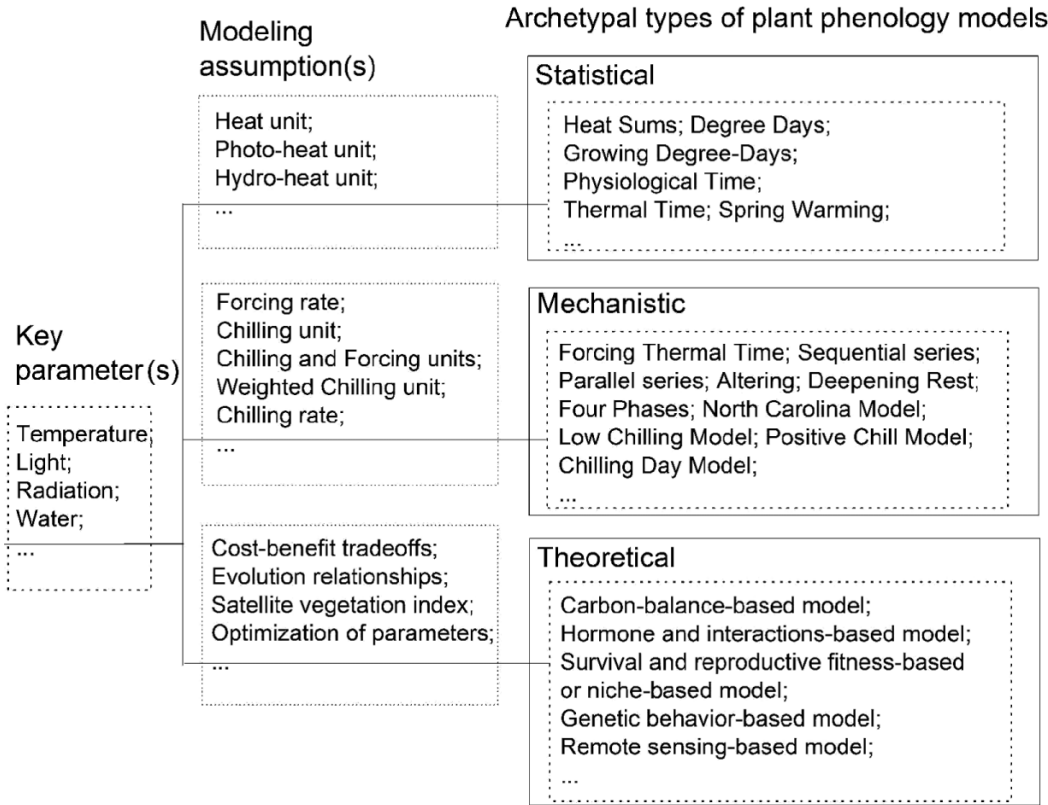
$$[1] \quad \sum U_t = \sum_{Date_0}^{Date_x} f(T_x, T_b) = \text{Heat}_{\text{critical}}$$

where  $Date_x$  is the timing of the plant phenological event;  $T_x$  is the daily mean temperature;  $T_b$  is the threshold or base temperature;  $Date_0$  is the day when heat unit starts to accumulate; and  $\text{Heat}_{\text{critical}}$  is the heat requirements.

Despite being widely applied and well-suited to regions and species, in the context of climate change, specifying biological processes defeats the purpose of modeling plant phenology as simple climate-dependent regressions or accumulations (e.g., Picard et al. 2005; Arora and Boer 2005). When this is the case,



Fig. 2. Diagram illustrating the three archetypal types of plant phenology models: statistical, mechanistic, and theoretical.



more mechanistic and process-oriented plant phenology models would be helpful in overcoming the abovementioned problems.

### 3.2. Mechanistic approach

Mechanistic or dynamic plant phenology models formally describe the known or assumed “cause–effect relationships” between biological processes and key driving variables present in the environments of plants. The data used to derive the “assumed cause–effect relationships” in mechanistic or dynamic plant phenology models is limited to the observed record. Most existing plant phenology models are of this type (Table A1). Onset models are one example. They assume that budburst occurs when a critical state of forcing temperature is reached, the state of forcing being the sum of the daily rate of forcing, which is solely a function of temperature (Chuine et al. 1999) (e.g., forcing Sarvas or forcing Thermal Time). For most tree species, the dormancy (rest) state must end before plants enter phases of quiescence. The rate of development during both phases has been related to temperature in many ways. It is typically referred to as chilling and forcing units of development (Kramer 1994). The chilling and forcing unit signifies that models are fitted to “spring onset” such as the Sequential model, the Parallel model, the Alternating model, the Deepening Rest model, the Four Phases model (Cannell and Smith 1983; Murray et al. 1989; Hänninen 1990; Kramer 1994) as well as certain other modeling improvements (e.g., Hänninen 1990, 1995; Kramer 1994; Chuine et al. 1999; Chuine 2000). These models can be written as

$$[2] \quad \sum_{Date_2}^{Date_z} R_t \sum_{Date_1}^{Date_y} R_{photo} \sum_{Date_0}^{Date_x} R_w \dots \sum R_{phy} = f(Phy_{x,y,z,\dots}, W_x, Photo_y, T_z, \text{Critical}^*, A^*, \dots)$$

where Date<sub>x</sub>, Date<sub>y</sub>, and Date<sub>z</sub> are the timing of the plant phenological event or phenol phases; Phy is the biological process; Phy<sub>x,y,z</sub> is the “cause–effect relationships” between assumed from essential physiology elements and key environmental driving variables; W, Photo, and T are the key driving factors for water, photoperiod, and temperature, respectively; W<sub>x</sub> is the soil water availability; Photo<sub>y</sub> is the photoperiodic cues; T<sub>z</sub> is the daily mean temperature; Date<sub>0</sub>, Date<sub>1</sub>, and Date<sub>2</sub> are the day when phenological events or phenol phases start; R<sub>t</sub>, R<sub>photo</sub>, R<sub>w</sub>, and R<sub>phy</sub> are the impact rates of development from temperature, photoperiod, water, and physiology elements, respectively; **Critical**<sup>\*</sup> is the critical vector of impact requirements; and A<sup>\*</sup> is the matrix of fitted constant parameters.

Obviously, parameters of these models have physical dimensions that can, in principle, be measured directly instead of being estimated by a fitting process. However, this is rarely possible. Experimental approaches and statistical model-fitting techniques are often used for parameter estimations in mechanistic or dynamic approaches. For the assortment of models, developmental responses to temperature during dormancy and quiescence have been described by various types of functions, i.e., the weighted chilling unit models such as the Utah model (Richardson et al. 1974), the North Carolina model (Gilreath and Buchanan 1981), the low chilling model (Shaulout and Unrath 1983), the positive chill unit model (Linsley-Noakes et al. 1995), and the chill day model (Cesaraccio et al. 2002), etc. Each of these proposes a range of effective temperatures and incorporates an optimum temperature for rest completion.

### 3.3. Theoretical approach

Based on the assumption of the cost–benefit tradeoff of producing leaves to optimize resource acquisition and that it was designed to understand the evolution of leaf strategies in trees

rather than annual variation in plant phenology, theoretical plant phenology models has been attempted in the development of modeling on various process-based or physiological aspects, i.e., reproductive fitness based processes or survival fitness based genetic behavior. Examples of these are the carbon balance based model, the hormone actions and interactions based model, the survival and reproductive fitness based model, the species range niche-based model, the genetic behavior based model, and the remote sensing based model, etc. (see Table A1 and Fig. 2).

### 3.3.1. Carbon balance based plant phenology model

The carbon-balance approach is theoretically based on plant physiological processes in that the carbon balance between leaf photosynthesis gains (carbon gain) and respiratory costs (carbon cost) determines leaf onset and offset times. This approach has been widely applied to leaf phenological parameterization in many ecosystem models such as the Frankfurt biosphere model by Lüdeke et al. (1994), the model developed by Kikuzawa (1995), the ecosys model by Grant et al. (1999), the Canadian Terrestrial Ecosystem Model by Arora and Boer (2005), the global terrestrial carbon cycle model by SILVAN (Kaduk and Heimann 1997), the BALANCE model (Rötzer 2005), and the DORMPHOT model (O'Neill et al. 2010). Although these approaches offer the possibility of reduced empiricism, general applicability, and increased robustness under global climate change conditions, they cannot avoid using certain direct empirical relationships that occur between climatic variables (temperature, moisture, etc.) and phenological events (Bondeau et al. 1999; Arora and Boer 2005).

### 3.3.2. Hormone actions and interactions based plant phenology model

The hormone actions and interactions based model triggers events after meeting critical thresholds that are either constant or dependent on environmental conditions or internal variables. Those mechanized for internal hormone states agree that the hypothesized balance or ratio between promoter and inhibitory agents determines the physiological state of development of a plant and its reaction to external driving forces (e.g., Powell 1987). An example of this is the abundance or concentration of enzymes assumed by the promoter–inhibitor model by Schaber and Badeck (2003).

### 3.3.3. Survival and reproductive fitness based or niche based plant phenology model

Formulating plant phenology and resistance to abiotic stresses such as frost and drought are key processes in determining species niche and, thereby, distribution. Survival and reproductive fitness based or niche based plant phenology models are based on the concept of fitness. They aim to estimate the survival and reproductive success of an average individual of a given population of tree species. In addition, they try to identify those traits that determine the fitness of individuals of species subjected to particular environmental conditions (Chuine and Beaubien 2001; Morin et al. 2007; Chuine 2010). Examples of this type are the gap models (Bugmann 2001), the landscape models (Scheller et al. 2007), PHENOFIT (Chuine and Beaubien 2001), the flower pollination component of the Alfalfa Seed Pollination model (Strickler 2007), etc. Survival and reproductive fitness based or niche based plant phenology models are powerful tools to provide predictions within the short-term. Their weakness, however, is that they may provide inaccurate predictions in the long-term (Thuiller 2007).

### 3.3.4. Genetic behavior based plant phenology model

Variations in different genetic pathways can be linked to phenology and life-history variation across geographical regions and seasons. Expressions of phenological traits such as flowering critically depend on growth season (Wilczek et al. 2010). In particular,

models that integrate and balance the importance of different environmental cues should obviate some of the problems associated with behavioral predictions under no-analog climates of the future (Williams and Jackson 2007). Based on the considerable understanding of the flowering time network and extensive natural variation in flowering time genes, the plant phenology model by Wilczek et al. (2009) proved to be an ideal model in which to explore links between genetic factors and phenological responses. It is capable of explaining a great deal of the observed phenological behavior for a variety of genetic backgrounds, seasons, and geographical locations.

### 3.3.5. Remote sensing based plant phenology model

For large-scale analysis, numerous studies have used the high-frequency coverage of the terrestrial biosphere supplied by the National Oceanic and Atmospheric Administration, advanced very high resolution radiometer, and, more recently, the moderate resolution imaging spectroradiometer to quantify ecosystem vegetation phenology (e.g., Zhang et al. 2006). Satellite vegetation index data such as the normalized difference vegetation index (NDVI) in combination with several biophysical parameters provide an efficient means to monitor regional- or global-scale phenology (e.g., Fisher et al. 2007). Two examples are the growing season index (Jolly et al. 2005) and the spring warming model (Migliavacca et al. 2008). Compared with species-specific phenology models, satellite data are especially useful in detecting mean phenological changes within each grid cell where diverse vegetation types are aggregated (White et al. 2002). This is an appropriate strategy for model parameter estimates that should be tailored to each vegetation community and plant species, geographic location, and scale level (e.g., Baldocchi et al. 2005). Certain methods such as inverse modeling or look-up tables are considered very useful for the optimization of model parameters in remote sensing based plant phenology models (e.g., Migliavacca et al. 2008; Peng et al. 2011).

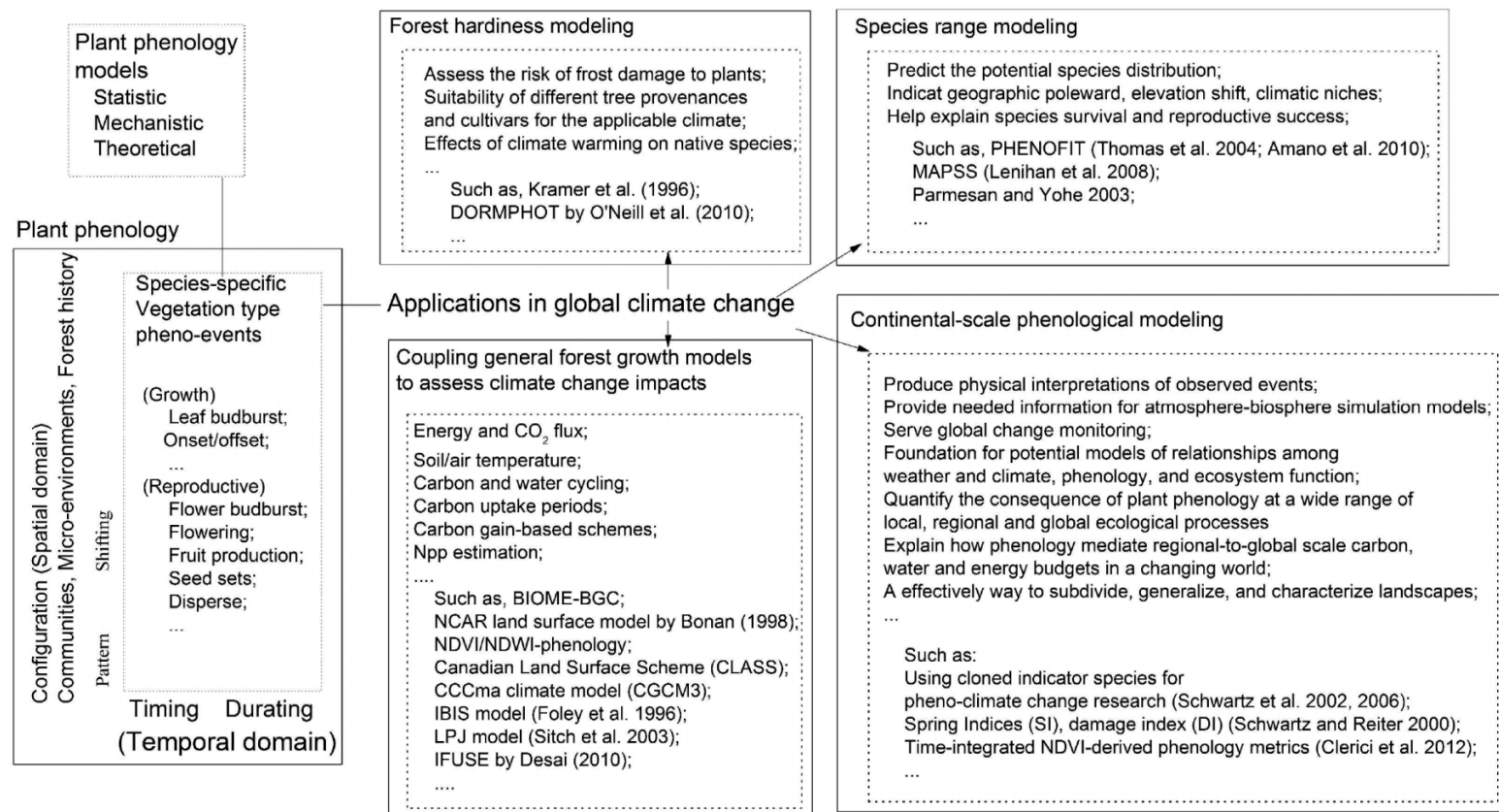
## 4. Plant phenology model applications used in global climate change studies

Plant phenology model is an important tool for the investigation of a wide range of global climate change related issues such as the prediction of global climate change impacts on plant phenology, models in development for the improvement of primary productivity, predicting the occurrence of pollen in the atmosphere (and thus occurrences of pollen allergies), and to support foresters and farmers in managerial decisions (e.g., Nord and Lynch 2009; Chuine 2010) (Fig. 3).

### 4.1. Forest hardiness modeling

With regard to phenology and spring frost damage, species differed in the extent to which the date of leaf unfolding advanced under conditions of increased winter temperatures and, thus, in the frequency of freezing temperatures to which they were subjected to at this approximate date (Kramer et al. 1996; Augspurger 2010). Such a differential response enhances existing differences between species under climate change conditions (Augspurger 2010). This may result in consequences in relation to the occurrence of frost damage and competition for light. Therefore, by evaluating relationships between temperature and both leaf unfolding and leaf fall as well as the progression of frost hardiness, both direct effects of climatic warming (on frost damage) and indirect effects (on competitive capacity) are accounted for (Cook et al. 2010). Plant phenology models of budburst have been frequently applied to assess the risk of frost damage to plants (Picard et al. 2005; Cook et al. 2010), both the suitability of different tree provenances and cultivars for the applicable climate (Hari and Häkkinen 1991) and the effects of climate warming on native tree

Fig. 3. Plant phenology model applications used in global climate changes.





species (Kramer et al. 1996). Leinonen (1996) developed several approaches related to hardiness and frost damage modeling over a calendar year, not only around times of budburst. Plant phenology model evaluations of climate change scenarios by Kramer et al. (1996) on three phenological types of deciduous trees and the effects of occurrences of frost damage on the growth of mixed-species forests indicated that differences in net primary production of the three phenological types under consideration will be enhanced when grown in a mixed-species stand compared with a monospecies stand, and the effects of frost damage on growth will be more prominent in mixed-species stands than in monospecies stands. O'Neill et al. (2010) applied a theoretical process-based model (DORMPHOT) on seven existent datasets from different European countries (Ireland, Germany, Switzerland, and Norway). Results showed good modeling competency and low mean absolute error, outperforming the currently used budburst models for birch.

#### 4.2. Coupling general forest growth models to assess climate change impacts

The timing of plant phenological phases is strongly reliant on terrestrial carbon and water cycling as well as atmospheric CO<sub>2</sub> concentrations (e.g., Peñuelas and Filella 2001). In addition, the magnitude of response of forest primary productivity varies with the particular plant phenology models applied (Leinonen and Kramer 2002; Vitasse et al. 2011). In the simplest case, effects of leaf phenology on energy and CO<sub>2</sub> flux is represented by prescribing leaf onset and offset times or the seasonal evolution of the leaf area index (LAI) (Chase et al. 1996). Typically, empirical growth degree day based models are often used to track phenological phases in land-surface models for carbon uptake periods (Baldocchi et al. 2005; Delpierre et al. 2009; Vitasse et al. 2011) or carbon gain based schemes (Arora and Boer 2005). Taking this into account, the BIOME-BGC model (Running and Hunt 1993) used specified leaf onset and offset dates for its three vegetation types. The National Center for Atmospheric Research community land surface model by Bonan (1998) used prescribed vegetation phenology dependent monthly values of LAI at each global climate model grid cell. Kaduk and Heimann (1996) presented prognostic and mechanistic schemes to determine plant phenological stages from environmental conditions as well as estimations of net primary production. Botta et al. (2000) proposed a global prognostic scheme for phenological dates in relation to NDVI or normalized difference water index data to estimate leaf onset times and develop empirical formulae to predict the dynamics of leaf phenology. Delbart et al. (2005) applied growth degree days and soil moisture-based leaf onset for extratropical and tropical biomes, respectively. Finally, de Beurs and Henebry (2010) applied spatio-temporal statistical methods to model land surface phenology. Some slightly more complex representations of plant phenology models adopt modeling approaches in which LAI varies between specified vegetation dependent maximum and minimum values, and where the timing of leaf onset and offset is a function of the soil/air temperature (e.g., Knorr 2000; Baldocchi et al. 2005) such as the Canadian Land Surface Scheme, the Canadian Centre for Climate modelling and analysis coupled global climate model, the integrated biosphere simulator model (Foley et al. 1996), and the Lund-Potsdam-Jena dynamic global vegetation model (Sitch et al. 2003). In the context of climate change, the carbon-balance phenological scheme that couples biosphere or ecosystem models such as the Frankfurt biosphere model by Lüdeke et al. (1994), the ecosys model by Grant et al. (1999), the Canadian Terrestrial Ecosystem Model by Arora and Boer (2005), the forest carbon model by photosynthetic/evapotranspiration model (Chiang and Brown 2007), or the Interannual Flux-tower Upscaling Sensitivity Experiment by Desai (2010) successfully specifies the seasonal evolution

of LAI or leaf onset and offset, but it defeats the purpose of modeling plant phenology as a dynamic climate-dependent process.

#### 4.3. Species range modeling

Understanding species distribution has become critically important for biodiversity conservation in the context of changing climate and the increasing fragmentation of natural habitats (Channell and Lomolino 2000). Species living in a fragmented or discontinuous habitat form a web of interconnected entities. Invasive species are frequently viewed as harbingers of climate change owing to their potential to cause economic and ecological damage while expanding their ranges (Clements and Ditommaso 2011). Many plant phenology models exist, (e.g. PHENOFIT) that have been widely used in the last 10 years to predict the potential impacts of both climate and land use changes on species distribution throughout the world (e.g., Thomas et al. 2004; Amano et al. 2010). These models have indicated that a geographic poleward and elevation shift is occurring in climatic niches for many species and can explain how plant phenology affects survival and reproductive success (e.g., Chuine and Beaubien 2001; Thomas et al. 2004; Morin et al. 2007; Morin and Thuiller 2009; Chuine 2010). The Mapped Atmosphere Plant Soil System Study has also reported on a global poleward migration of plant life due to conditions of climate change. This includes a northward migration of vegetation in the United States of America (Lenihan et al. 2008) and range shifts for 99 plants and animals of various countries in the Northern Hemisphere (Parmesan and Yohe 2003).

#### 4.4. Continental-scale phenological modeling

Understanding the interaction between the atmosphere (weather and climate) and the biosphere (living organisms) is a necessary part of efforts to improve models of Earth's physical systems and monitor the impact of global climate change (Schwartz 1998; Hayhoe et al. 2007; Cleland et al. 2007). For continental scale, plant phenology models serve satellite bioclimatology in concert with surface phenology can produce physical interpretations of observed events, providing needed information for atmosphere-biosphere simulation models and global change monitoring. Improved plant or vegetation phenological modeling at a local- or regional-scale to continental-scale would provide a foundation for potential models of relationships among weather and climate, phenology, and ecosystem function (Richardson et al. 2012). This will improve our knowledge and understanding of the way ecosystems "work", how plant phenology responds to climate variability and change (Peñuelas et al. 2009). The continental-scale phenological modeling approaches using cloned indicator species (such as the lilac and honeysuckle) have demonstrated their usefulness for phenoclimate change research in numerous ways (Schwartz et al. 2006). For example, they are able to practically provide greater insight into spatial and temporal patterns of variation across a range of forest and (or) vegetation types. At first the continental-scale phenological modeling approaches were optimized for continental-scale studies and providing a ready means to process climate data into a form comparable with satellite sensor derived and conventional phenological data (Schwartz et al. 2002, 2006). In the process for the development and refinement of phenological simulation models (Schwartz 1993), the "first approximation of a comprehensive spring index" was proposed based on an averaging of the modeled dates of first leaf models for the lilac and honeysuckle indicators (Schwartz 1990), a first leaf model derived "spring index" facilitated reconstructing past phenological responses in eastern North America (Schwartz 1993); the "damage index", first spring leaf date minus last spring frost date, were calculated to assess the risk of frost damage to spring plant development; the "spring indices suite of measurements" (Schwartz and Reiter 2000), calculations expanded to include an extensive range of measures, was intro-

duced to evaluate the general impact of climate change on the onset of spring in North America, China, and across temperate regions of the Northern Hemisphere (Schwartz et al. 2006); and produced measures of phenological development over large areas, using networked digital cameras, or webcams, as multichannel (red, green, and blue color channels) imaging sensors with which the development, senescence, coloration and abscission of forest canopies can be continuously tracked, that can be compared with and provide a means to offer opportunities to bridge the spatial gap between ground-based phenology and satellite-derived indices and assess the accuracy of satellite sensor derived phenological products (Kathuroju et al. 2007; Schwartz and Hanes 2010a, 2010b). In addition, the continental-scale phenological modeling approaches attempt to understand and quantify the consequence of plant phenology at a wide range of local, regional, and global ecological processes, and how they mediate regional-to-global scale carbon, water, and energy budgets in a changing world. The investigation of the profound effects of plant phenology on energy and mass exchange, and measured air characteristics in the lower atmosphere, are ultimately related to variations in the surface energy balance and have implications for carbon dioxide flux (e.g., net ecosystem exchange) and balance (Schwartz and Crawford 2001). These may be crucial for accurate scaling-up of flux measurements or downscaling of atmospheric circulation models. Cayan et al. (2001) established the connection of plant phenology to temperatures and stream runoff in the western USA. The time-integrated, NDVI-derived phenology metrics can also provide effective ways to subdivide, generalize, and characterize landscapes, such as modeling the trends in growing season length (Myneni et al. 1997); separating herbaceous from woody vegetation cover (Lu et al. 2003); identification and mapping of forest general habitat categories (Clerici et al. 2012); and continental estimations of biophysical parameters, such as gross primary production (Jung et al. 2008). All these effects will be helpful for better understanding the temporal-spatial variability of the carbon and water exchanges (Clerici et al. 2012). van Leeuwen et al. (2010) explored the use of land surface phenological metrics for assessing postfire vegetation response in Spain, Israel, and USA.

## 5. Limitations

Researchers have used numerous techniques to evaluate how plant phenology has shifted in recent decades. Moreover, developments in plant phenology models have increased our understanding of plant phenology at a molecular level (Sung and Amasino 2004). There are many aspects in plant phenology modeling and application that remain to be understood, which limits a thorough and comprehensive understanding of plant phenology. This knowledge gap reduces our capacity to interpret observations and make meaningful projections in relation to disturbances and their subsequent impacts. It also limits the development of strategies required to intervene in ecosystem response to abiotic and biotic interactions.

### 5.1. Uncertainties relating to mechanisms that regulate plant phenology

Responses of plant phenology vary owing to confounding factors (e.g., land use change and urbanization), different aspects of the climate as a driving mechanism, species interactions, different boundaries of the same species, and certain evidence related to the asymmetry of response across trophic levels (Parmesan 2007). Mechanisms of plant phenology are only beginning to emerge. Many uncertainties remain: (1) uncertainties with regard to how important specific environmental factors are in determining plant phenology, the precise molecular and physiological processes regulating plant phenology, and whether variation in plant phenology over time or among individuals reflects genetic differ-

ences or is simply plastic responses to environmental heterogeneity; and (2) uncertainties with regard to how abiotic and biotic factors interact on a mechanistic level (see Forrest and Miller-Rushing 2010). For example, existing plant phenology models have focused mostly on climate change induced impacts and plant phenology responses. They have rarely been concerned with relationships between phenological events and biotic (abiotic) conditions or correlations between phenological events of the same or different plant species. Pest phenology can provide information concerning the life-cycle trend of a pest, and sets of conditions (environmental variables) for which critical events, such as a transition to a certain developmental stage or relevant increase in the number of pest individuals within a certain developmental stage, can appear. To date, plant phenology model approaches have not yet considered these indicators. However, since only one regulatory mechanism exists for a certain plant species, the authenticity of modeling results may be validated by using different plant phenology models to simulate the same phenol phases of the same plant species. Rapid progress is being made in the area of plant phenology models to address uncertainties that relate to mechanisms that regulate plant phenology, but, for now, they substantially limit our ability to anticipate future responses of plant phenology to changes in climatic variables (e.g., Visser et al. 2010; Wilczek et al. 2010).

### 5.2. Uncertainties relating to model parameterization

The parameterization process is also a factor that restricts the development of plant phenology models. Better parameterization promotes an increase in modeling authenticity (Chuine et al. 1998). Many phenological models have been fitted locally, fitted to a species-specific application, or restricted to several species applications. Universality of plant phenology models has not been widely studied (Chuine 2000; Diez et al. 2012). Over the last decades, extreme weather has more pronounced changes than average weather, and species and ecosystems have responded more rapidly to this more complex set of changes than the average climate change in most climate scenarios. Unfortunately, extreme events are rarely considered in most model-based impact studies (van Vliet 2010). Phenological events associated with cultivation are not only controlled by climate change but are also severely affected by anthropogenic activity and field management measures and practices (Zhang et al. 2003). However, little research has been conducted to identify the relative contribution of these anthropogenic factors because of the complex interaction of these mechanisms (Piao et al. 2006). Modeling endeavors currently being practiced in state-of-the-art land surface schemes are inadequate for resolving the complexities of surface-atmosphere exchanges associated with plant phenology (Kucharik et al. 2006; Morin et al. 2008). Coupled, dynamic, and global vegetation-climate models either specify a predetermined phenological scheme or produce phenological parameters as an output of the model. When predetermined, phenology is not responsive to environmental drivers; and when driven by the model, predictions in phenology tend to be biased because models use a limited number of plant functional types that overly simplify representations of ecosystem processes (e.g., Fisher et al. 2007). Process-based models bridge the gap between the extensive spatial scales available from satellite-derived observational data and link themselves to driving variables that can potentially be derived from ground observations, often species-specific and calibrated to local scales (Ibáñez et al. 2010). Nevertheless, potential confusion and bias still exist in relation to how to calculate phenological transition times due to the mix of methods and definitions being used (White and Nemani 2003).



### 5.3. Uncertainties related to future climate change predictions

To predict feedbacks of plant dynamics to future climate systems, the inclusion of plant phenology models appear crucial despite certain inherent predicting uncertainties (Diez et al. 2012). Current state-of-the-art climate models seldom include any aspects of plant phenology models that would incorporate relevant ecophysiological knowledge into the model. Multispecies interactions, fundamental regulations of biodiversity, and the impact of environmental changes on plant communities have all been altered in relation to the way species respond to global climate change (Parmesan 2007). Accordingly, plant phenology models based on the “species–area relationship” would project the future geographic range of a species from the current distribution of a species mapped in climate space. This approach fails to include critical types of species interactions, even though current (and future) distributions of species that reflect these fundamental influences leave much of the more detailed variation in community composition unexplained (Botkin et al. 2007; Voigt et al. 2007). Also, by its very nature, plant life is a multispecies interactive network. Plant components in terrestrial ecosystems both aboveground and belowground are interlinked, and these interactions can differ in strength and sign, either positive (facilitation), negative (inhibition) or neutral (Post and Pedersen 2008). Changes in the relative distribution of organisms not only alter species composition and food web structure but also initiate changes in ecosystem function (Post and Pedersen 2008). Monte Carlo techniques have been applied to try to address question of uncertainty in phenological forecasts (Richardson et al. 2010), uncertainty relating to future phenological responses to climate change, and the associated effects on ecosystem health and biogeochemical cycling. Despite these attempts, uncertainties have not been rigorously quantified. Much needs to be done to improve phenological model predictions. Improvements will have to be grounded on a deeper understanding of plant ecophysiological processes. Even so, problems will likely continue into the future. Modeled niche results derived from niche-based plant phenology models will be projected into future states and conditions using data from general circulation models or regional climate models and by highlighting areas that are deemed suitable. However, suitability will become incompatible under predicted future climate change states and conditions and vice versa (Ohlemüller et al. 2006).

### 6. Challenges and future prospects

Rapid progress is being made in the area of plant phenology models to address uncertainties in relation to plant phenology. Uncertainties will complicate efforts made in the area of model phenological responses to ongoing climate change; but to build reliable forecasts in the future, it must be incorporated (e.g., Visser et al. 2010; Wilczek et al. 2010; Ibáñez et al. 2010). The precise prediction of reoccurring times of phenological events will require seasonal dynamics of LAI and knowledge of how different types of vegetation respond to climate change. Below are suggestions to strengthen model performance.

- (1) Improve methods in phenological observational data collection and experimental data analysis (e.g., synthetic analytical techniques offered by remote sensing or geographic information system could be used to analyze the time series and spatial variation of phenological data).

The lack of observational data from the phenol-phase process from start to end can be offset by anatomical or biochemical techniques that could be used to ascertain or mark the middle stage. The process of analyzing field observational data collected from nonnatural locations such as botanical gardens, arboreturns, parks or city green belts should also include the urban heat island effect. Moreover, future analysis

should include near daily measurements using LAI-2000 or similar field instrumentation during both the spring and autumn seasons (senescence) to bring together a more comprehensive record. More expansive site analysis should include heterogeneous coverage, the effects of scaling site level measurements (field or high-resolution remote sensing) to the region under investigation, and the contribution of ground reflectance. The local populace could be encouraged to collect data. This would considerably increase datasets. It should be noted that many citizen scientists are prepared for environmental conditions in areas in which they live. They could be directed to observe a very specific research area such as trees, flowers buds, etc. and dispatch their field observations back to a central plant phenology model database. The USA National Phenology Network is a good example for the plant phenology model database (Betancourt et al. 2005, 2007). This would undoubtedly help a small number of researchers track a large quantity of reliable field data that they would otherwise not be able to gather on their own. It would also help guarantee the authenticity of plant phenology models.

- (2) Promote research on physio-ecological mechanisms that drive phenological events while clarifying phenological driving factors and mechanisms for different types of vegetation to offer a theoretical basis and verification data to the phenological parameterization process of biome models (Schwartz et al. 2006; Richardson et al. 2010).
- (3) Analyze the climate change response processes, mechanisms of phenological events, and LAI dynamics to provide evidence to model the effects of climate change on vegetation structure and dynamics. Establish general phenological parameterization schemes on the basis of a better understanding of physio-ecological mechanisms of phenological events for different vegetation types, while coupling phenological subroutines to ecosystem models to address more accurately how climate change in the future will influence terrestrial ecosystem productivity as well as water and CO<sub>2</sub> flux (Alessandri et al. 2007; Kathuroju et al. 2007; Steiner et al. 2009; Richardson et al. 2010, 2012).
- (4) Current studies have mostly focused their attention on the response of plant phenological change to climatic change. It should be noted that other factors such as heredity or pests, plant and animal phenological adaptation and interactions, and ecological disturbances such as forest fires and insect outbreaks may also affect phenological events (Amano et al. 2010; Kaduk and Los 2011; Vitasse et al. 2011). These factors, however, have seldom been considered in the past. It must be concluded at this point that broadening the research scope may result in a breakthrough in future studies on plant phenology models. The prediction of spring leaf onset by means of long-term forecasting would dramatically aid in model development (Arora and Boer 2005).
- (5) Include the possibility that other often unmeasured microenvironmental factors (like soil temperature, etc.) may play a role in affecting phenological variations over space, and that more extensive environmental gradients could lead to stronger impacts on spatial patterns of phenology as suggested by studies in other locations (Fisher et al. 2006; Liang and Schwartz 2009). Effects of anthropogenic drivers on phenological events associated with cultivation should be given more attention in future phenological studies (Wu et al. 2008).
- (6) Phenological modeling may benefit from advancing parameterization approaches such as machine learning techniques and data assimilation, while at the same time addressing issues related to nonlinear and discontinuous phenomena. Furthermore, the introduction of more nonlinearities into model simulations could further reduce uncertainties and bias.

## 7. Conclusions

Natural ecosystems are undergoing phenological shifts due to a changing global climate. Many different kinds of plant phenology models have been developed and tested with varying degrees of success, built on the clear understanding of key parameters that trigger or control changes or shifts in plant phenological events. Taking into account the parameterization methods in existence, the three main types of plant phenology models are statistical, mechanistic, and theoretical approaches. The majority of plant phenology models in use are mechanistic or dynamic plant phenology models; however, each type has its advantages and shortcomings.

To date, most plant phenology models have been used to monitor vegetation, carbon accounting, species range modeling, climate change impact assessments, and biodiversity monitoring. For large-area vegetation type modeling efforts, land-surface remote sensing based plant phenology models can be used to qualitatively assess diagnostic global phenology datasets from past satellite observational periods or provide prognostic predictions on future climate dynamics.

Our understanding of plant phenology modeling and future climate change forecasting of plant phenology models remains limited. Some examples are (1) differing aspects of climate as driving mechanisms, species interactions, varying boundaries of a single species, and evidence that suggests asymmetry of response across trophic levels; (2) variation in species phenological responses to changing climate conditions owing to confounding factors (land use change and urbanization); (3) estimation of uncertainty related to model structure and parameterization based on variability among models and across posterior parameter distributions, respectively; (4) uncertainties of future phenological responses to climate change and the associated effects on ecosystem health and biogeochemical cycling, and, in particular, uncertainties that have not as yet been rigorously quantified.

These uncertainties complicate efforts in predicting phenological responses to ongoing climate change conditions, but they must be incorporated to build reliable forecasts. At present, plant phenology models based on plant physio-ecological processes remains insufficient. Plant phenology models must begin to incorporate process-based model leaf phenology and LAI features to promote future simulation robustness. With ongoing studies related to plant physio-ecological processes, a trend should inevitably surface among researchers to establish plant physio-ecological process-based phenological models for terrestrial ecosystems.

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## References

- Alessandri, A., Gualdi, S., Polcher, J., and Navarra, A. 2007. Effects of land surface-vegetation on the boreal summer surface climate of a GCM. *J. Clim.* **20**(2): 255–278. doi:10.1175/JCLI3983.1.
- Amano, T., Smithers, R.J., Sparks, T.H., and Sutherland, W.J. 2010. A 250-year index of first flowering dates and its response to temperature changes. *Proc. R. Soc. B*, **277**(1693): 2451–2457. doi:10.1098/rspb.2010.0291.
- Arora, V.K., and Boer, G.J. 2005. A parameterization of leaf phenology for the terrestrial ecosystem component of climate models. *Global Change Biol.* **11**: 39–59. doi:10.1111/j.1365-2486.2004.00890.xrsb20100291.
- Augsburger, C.K. 2010. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. *Funct. Ecol.* **23**(6): 1031–1039. doi:10.1111/j.1365-2435.2009.01587.x.
- Ault, T.R., Macalady, A.K., Pederson, G.T., Betancourt, J.L., and Schwartz, M.D. 2011. Northern Hemisphere Modes of Variability and the Timing of Spring in Western North America. *J. Climate*, **24**: 4003–4014. doi:10.1175/2011JCLI4069.1.

- Badeck, F.W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., and Sitch, S. 2004. Responses of spring phenology to climate change. *New Phytol.* **162**: 295–309. doi:10.1111/j.1469-8137.2004.01059.x.
- Baldocchi, D.D., Black, T.A., Curtis, P.S., Falge, E., Fuentes, J.D., Granier, A., Gu, L., Knohl, A., Pilegaard, K., Schmid, H.P., Valentini, R., Wilson, K., Wofsy, S., Xu, L., and Yamamoto, S. 2005. Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. *Int. J. Biometeorol.* **49**: 377–387. doi:10.1007/s00484-005-0256-4. PMID:15688192.
- Beaubien, E.G., and Freeland, H.J. 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature. *Int. J. Biometeorol.* **44**: 53–59. doi:10.1007/s004840000050. PMID:10993558.
- Betancourt, J.L., Schwartz, M.D., Breshears, D.D., Brewer, C.A., Frazer, G., Gross, J.E., Mazer, S.J., Reed, B.C., and Wilson, B.E. 2007. Evolving Plans for the U.S.A. National Phenology Network. *EOS*, **88**(19): 211–211. doi:10.1029/2007EO190008.
- Betancourt, J.L., Schwartz, M.D., Breshears, D.D., Cayan, D.R., Dettinger, M.D., Inouye, D.W., Post, E., and Reed, B.C. 2005. Implementing a U.S. National Phenology Network. *EOS*, **86**(51): 539–541. doi:10.1029/2005EO510005.
- Bonan, G.B. 1998. The land surface climatology of the NCAR land surface model (LSM 1.0) coupled to the NCAR Community Climate Model (CCM3). *J. Climate*, **11**: 1307–1326. doi:10.1175/1520-0442(1998)011<1307:TLSCOT>2.0.CO;2.
- Bondeau, A., Kicklighter, D.W., and Kaduk, J. 1999. Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. *Global Change Biol.* **5**(Suppl. 1): 35–45. doi:10.1046/j.1365-2486.1999.00005.x.
- Borchert, R., and Rivera, G. 2001. Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiol.* **21**: 213–221. doi:10.1093/treephys/21.4.213. PMID:11276415.
- Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R., Cedhagen, T., Chesson, P., Davis, M.B., Dawson, T.P., Etterson, J., Faith, D.P., Ferrier, S., Guisan, A., Skjoldborg, A., Hansen, D.H., Kareiva, P., Loehle, M.C., New, M., Skov, F., Sobel, M.J., Stockwell, D., and Svenning, J.C. 2007. Forecasting the effects of global warming on biodiversity. *Bioscience*, **57**(3): 227–236. doi:10.1641/B570306.
- Botta, A., Viovy, N., Ciais, P., Friedlingstein, P., and Monfray, P. 2000. A global prognostic scheme of leaf onset using satellite data. *Global Change Biol.* **6**: 709–725. doi:10.1046/j.1365-2486.2000.00362.x.
- Bugmann, H. 2001. A review of forest gap models. *Clim. Change*, **51**: 259–305. doi:10.1023/A:1012525626267.
- Cannell, M.G.R., and Smith, R.I. 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *J. Appl. Ecol.* **20**: 951–963. doi:10.2307/2403139.
- Cayan, D.R., Kammerdiener, S., Dettinger, M., Caprio, J., and Peterson, D. 2001. Changes in the onset of spring in the western United States. *Bull. Am. Met. Soc.* **82**: 399–415. doi:10.1175/1520-0477(2001)082<0399:CITTOOS>2.3.CO;2.
- Cesaraccio, C., Snyder, R.L., Spano, D., and Duce, P. 2002. A new model for estimating chill accumulation requirements for crop and natural species. *In* Proceedings of the 25th Agricultural and Forest Meteorology Conference: Norfolk, VA, 20–24 May 2002. *Am. Meteorol. Soc.* pp. 111–112.
- Chambers, L.E., and Keatley, M.R. 2010. Phenology and climate — early Australian botanical records. *Aust. J. Bot.* **58**(6): 473–484. doi:10.1071/BT10105.
- Channell, R., and Lomolino, M.V. 2000. Dynamic biogeography and conservation of endangered species. *Nature*, **403**(6765): 84–86. doi:10.1038/47487. PMID:10638757.
- Chase, T.N., Pielke, R.A., Kittel, T.G.F., Nemani, R., and Running, S.W. 1996. Sensitivity of a general circulation model to global changes in leaf area index. *J. Geophys. Res.* **101**: 7393–7408. doi:10.1029/95JD02417.
- Chiang, J.M., and Brown, K.J. 2007. Improving the budburst phenology subroutines in the forest carbon model PnET. *Ecol. Model.* **205**(3–4): 515–526. doi:10.1016/j.ecolmodel.2007.03.013.
- Chmielewski, F.M., Müller, A., and Bruns, E. 2004. Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961–2000. *Agric. For. Meteorol.* **121**: 69–78. doi:10.1016/S0168-1923(03)00161-8.
- Chuine, I. 2000. A unified model for budburst of trees. *J. Theor. Biol.* **207**: 337–347. doi:10.1006/jtbi.2000.2178. PMID:11082304.
- Chuine, I. 2010. Why does phenology drive species distribution? *Phil. Trans. R. Soc. B*, **365**: 3149–3160. doi:10.1098/rstb.2010.0142.
- Chuine, I., and Beaubien, E.G. 2001. Phenology is a major determinant of tree species range. *Ecol. Lett.* **4**: 500–510. doi:10.1046/j.1461-0248.2001.00261.x.
- Chuine, I., Cour, P., and Rousseau, D.D. 1998. Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell Environ.* **21**: 455–466. doi:10.1046/j.1365-3040.1998.00299.x.
- Chuine, I., Cour, P., and Rousseau, D.D. 1999. Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling. *Plant Cell Environ.* **22**: 1–13. doi:10.1046/j.1365-3040.1999.00395.x.
- Chuine, I., Yiou, P., Viovy, N., Seguin, B., Daux, V., Valérie, D., and Emmanuel, L. 2004. Historical phenology: grape ripening as a past climate indicator. *Nature*, **432**: 289–290. doi:10.1038/432289a. PMID:15549085.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A., and Schwartz, M.D. 2007. Shifting plant phenology in response to global change. *Trends Ecol. Evol.* **22**(7): 357–365. doi:10.1016/j.tree.2007.04.003. PMID:17478009.



- Clements, D.R., and Dittomasso, A. 2011. Climate change and weed adaptation: can evolution of invasive plants lead to greater range expansion than forecasted? *Weed Res.* **51**: 227–240. doi:10.1111/j.1365-3180.2011.00850.x.
- Cook, B.I., Terando, A., and Steiner, A. 2010. Ecological forecasting under climatic data uncertainty: a case study in phenological modelling. *Environ. Res. Lett.* **5**, 044014. doi:10.1088/1748-9326/5/4/044014.
- Clerici, N., Weissteiner, C.J., and Gerard, F. 2012. Exploring the use of MODIS NDVI-based phenology indicators for classifying forest general habitat categories. *Remote Sens.* **4**(6): 1781–1803. doi:10.3390/rs4061781.
- Črepinšek, Z., Kajfež-Bogataj, L., and Bergant, K. 2006. Modelling of weather variability effect on fitophenology. *Ecol. Model.* **194**: 256–265. doi:10.1016/j.ecolmodel.2005.10.020.
- Crimmins, T.M., Crimmins, M.A., and Bertelsen, D.C. 2010. Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. *J. Ecol.* **98**: 1042–1051. doi:10.1111/j.1365-2745.2010.01696.x.
- de Beurs, K.M., and Henebry, K.M. 2010. A land surface phenology assessment of the northern polar regions using MODIS reflectance time series. *Can. J. Remote Sens.* **36**(Suppl. 1): S87–S110. doi:10.5589/m10-021.
- Delbart, N., Kergoat, L., Toan, T.L., Lhermitte, J., and Picard, G. 2005. Determination of phenological dates in boreal regions using normalized difference water index. *Remote Sens. Environ.* **97**: 26–38. doi:10.1016/j.rse.2005.03.011.
- Delpierre, N., Soudani, K., François, C., Köstner, B., Pontailier, J.-Y., Nikinmaa, E., Priszter, S.Z., Aubinet, M., Bernhofer, C., Granier, A., Grünwald, T., Heinesch, B., Longdoz, B., Ourcival, J.-M., Rambal, S., Vesala, T., and Dufrene, E. 2009. Exceptional carbon uptake in European forests during the warm spring of 2007: A data-model analysis. *Global Change Biol.* **15**: 1455–1474. doi:10.1111/j.1365-2486.2008.01835.x.
- Desai, A.R. 2010. Climatic and phenological controls on coherent regional inter-annual variability of carbon dioxide flux in a heterogeneous landscape. *J. Geophys. Res.* **115**: G00J02, 13 pp. doi:10.1029/2010JG001423.
- Diez, J.M., Ibáñez, I., Miller-Rushing, A.J., Mazer, S.J., Crimmins, T.M., Crimmins, M.A., Bertelsen, C.D., and Inouye, D.W. 2012. Forecasting phenology: from species variability to community patterns. **15**(6): 545–553. doi:10.1111/j.1461-0248.2012.01765.x.
- Eppich, B., Dede, L., Ferenczy, A., Garamvölgyi, Á., Horváth, L., Isépy, I., Priszter, S.Z., and Hufnagel, L. 2009. Climate effects on the phenology of geophytes. *Appl. Ecol. Environ. Res.* **7**(3): 253–266. Available from [http://www.ecology.kee.hu/pdf/0703\\_253266.pdf](http://www.ecology.kee.hu/pdf/0703_253266.pdf).
- Fisher, J.L., Mustard, J.F., and Vadeboncoeur, M.A. 2006. Green leaf phenology at Landsat resolution: Scaling from the field to the satellite. *Remote Sens. Environ.* **100**: 265–279. doi:10.1016/j.rse.2005.10.022.
- Fisher, J.L., Richardson, A.D., and Mustard, J.F. 2007. Phenology model from surface meteorology does not capture satellite-based greenup estimations. *Global Change Biol.* **13**: 707–721. doi:10.1111/j.1365-2486.2006.01311.x.
- Foley, J.A., Prentice, I.C., Ramunkutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics (IBIS). *Global Biogeochem. Cy.* **10**(4): 603–628. doi:10.1029/96GB02692.
- Forrest, J., Inouye, D.W., and Thomson, J.D. 2010. Flowering phenology in sub-alpine meadows: Does climate variation influence community co-flowering patterns? *Ecology*, **91**(2): 431–440. doi:10.1890/09-0099.1. PMID:20392008.
- Forrest, J., and Miller-Rushing, A.J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philos. Trans. R. Soc. B.* **365**: 3101–3112. doi:10.1098/rstb.2010.0145.
- Galán, C., Carinanos, P., García-Mozo, H., Alcazar, P., and Dominguez-Vilches, E. 2001. Model for forecasting Olea europea L. airborne pollen in South-West Andalusia, Spain. *Int. J. Biometeorol.* **45**: 59–63. doi:10.1007/s004840100089.
- García-Mozo, H., Galán, C., Aïra, M.J., Belmonte, J., Díaz de la Guardia, C., Fernández, D., Gutierrez, A.M., Rodriguez, F.J., Trigo, M.M., and Dominguez-Vilches, E. 2002. Modelling start of oak pollen season in different climatic zones in Spain. *Agric. For. Meteorol.* **110**: 247–257. doi:10.1016/S0168-1923(02)00003-5.
- Gilreath, P.R., and Buchanan, D.W. 1981. Rest prediction model for low-chilling 'Sungold' nectarine. *J. Am. Soc. Hort. Sci.* **106**: 426–429. Available from <http://openagricola.nal.usda.gov/Record/IND81097862> [accessed 1985].
- Grant, R.F., Black, T.A., den Hartog, G., Berry, J.A., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., and Nalder, I.A. 1999. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: testing the mathematical model Ecosys with data from the BOREAS experiment. *J. Geophys. Res.* **104**(22): 27699–27717. doi:10.1029/1998JD200117.
- Häkkinen, R., Linkosalo, T., and Hari, P. 1995. Methods for combining phenological time series: application to bud burst in birch (*Betula pendula*) in Central Finland for the period 1896–1955. *Tree Physiol.* **15**: 721–736. doi:10.1093/treephys/15.11.721. PMID:14965990.
- Hänninen, H. 1990. Modelling bud dormancy release in trees from cool and temperate regions. *Acta For. Fenn.* **213**: 1–47.
- Hänninen, H. 1995. Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. *Can. J. Bot.* **73**(2): 183–199. doi:10.1139/b95-022.
- Hari, P., and Häkkinen, R. 1991. The utilization of old phenological time series of budburst to compare models describing annual cycles of plants. *Tree Physiol.* **8**: 281–287. doi:10.1093/treephys/8.3.281. PMID:14972878.
- Hayhoe, K., Wake, C., Huntington, T.G., Luo, L., Schwartz, M.D., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T.J., and Wolfe, D. 2007. Past and Future Changes in Climate and Hydrological Indicators in the U.S. Northeast. *Clim. Dynam.* **28**(4): 381–407. doi:10.1007/s00382-006-0187-8.
- Hopp, R.J. 1974. Plant phenology observation networks. In *Phenology and seasonality modelling*. Edited by H. Lieth. Springer, Berlin Heidelberg, New York. pp. 25–43.
- Hunter, A.H., and Lechowicz, M.J. 1992. Predicting the timing of budburst in temperate trees. *J. Appl. Ecol.* **29**: 597–604. doi:10.2307/2404467. Available from <http://www.jstor.org/stable/2404467>.
- Ibáñez, I., Primack, R.B., Miller-Rushing, A.J., Ellwood, E., Higuchi, H., Lee, S.D., Kobori, H., and Silander, J.A. 2010. Forecasting phenology under global warming. *Phil. Trans. R. Soc. B.* **365**: 3247–3260. doi:10.1098/rstb.2010.0120.
- Jolly, W.M., Nemani, R., and Running, S.W. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biol.* **11**: 619–632. doi:10.1111/j.1365-2486.2005.00930.x.
- Jung, M., Verstraete, M., Gobron, N., Reichstein, M., Papale, D., Bondeau, A., Robustelli, M., and Pinty, B. 2008. Diagnostic assessment of European gross primary production. *Global Change Biol.* **14**: 2349–2364. doi:10.1111/j.1365-2486.2008.01647.x.
- Kaduk, J., and Heimann, M. 1996. A prognostic phenology scheme for global terrestrial carbon cycle models. *Clim. Res.* **6**(1): 1–19. doi:10.3354/cr006001.
- Kaduk, J., and Heimann, M. 1997. Assessing the climate sensitivity of the global terrestrial carbon cycle model SILVAN. *Phys. Chem. Earth*, **21**(5–6): 529–535. doi:10.1016/S0079-1946(97)81153-6.
- Kaduk, J.D., and Los, S.O. 2011. Predicting the time of green up on temperate and boreal biomes. *Clim. Change* **107**: 277–304. doi:10.1007/s10584-010-9951-1.
- Kathuroju, N., White, M.A., Symanzik, J., Schwartz, M.D., Powell, J.A., and Nemani, R.R. 2007. On the use of the Advanced Very High Resolution Radiometer for development of prognostic land surface phenology models. *Ecol. Model.* **201**(2): 144–156. doi:10.1016/j.ecolmodel.2006.09.011.
- Kikuzawa, K. 1995. Leaf phenology as an optimal strategy for carbon gain in plants. *Can. J. Bot.* **73**: 158–163. doi:10.1139/b95-019.
- Knorr, W. 2000. Annual and interannual CO<sub>2</sub> exchanges of the terrestrial biosphere: process based simulations and uncertainties. *Global Ecol. Biogeogr.* **9**: 225–252. doi:10.1046/j.1365-2699.2000.00159.x.
- Kramer, K. 1994. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* **31**: 172–181. doi:10.2307/2404609.
- Kramer, K., Friend, A.D., and Leinonen, I. 1996. Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of mixed temperate-zone deciduous forests. *Clim. Res.* **7**: 31–41. doi:10.3354/cr007031.
- Kramer, K., Leinonen, I., and Loustau, D. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *Int. J. Biometeorol.* **44**: 67–75. doi:10.1007/s004840000066. PMID:10993560.
- Krzanowski, W. 1998. An introduction to statistical modeling. Oxford University Press Inc., New York, pp 252.
- Kucharik, C.J., Baeford, C.C., Maayar, M. E.Wofsy, S.C., Monson, R.K., and Baldocchi, D.D. 2006. A multi-year evaluation of a Dynamic Global Vegetation Model at three AmeriFlux forest sites: Vegetation structure, phenology, soil temperature, and CO<sub>2</sub> and H<sub>2</sub>O vapor exchange. *Ecol. Mod.* **196**: 1–31. doi:10.1016/j.ecolmodel.2005.11.031.
- Leinonen, I. 1996. A simulation model for the annual frost hardness and freeze damage of Scots pine. *Ann. Bot.* **78**: 687–693. doi:10.1006/anbo.1996.0178.
- Leinonen, I., and Kramer, K. 2002. Applications of phenological models to predict the future carbon sequestration potential of boreal forests. *Clim. Change*, **5**: 99–113. doi:10.1023/A:1020251507469.
- Lenihan, J.M., Bachelet, D., Neilson, R.P., and Drapek, R. 2008. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Clim. Change*, **87**: S215–S230. doi:10.1007/s10584-007-9362-0.
- Liang, L., and Schwartz, M.D. 2009. Landscape Phenology: An Integrative Approach to Seasonal Vegetation Dynamics. *Landscape Ecol.* **24**(4): 465–472. doi:10.1007/s10980-009-9328-x.
- Liang, L., Schwartz, M.D., and Fei, S. 2012. Photographic Assessment of Temperate Forest Understory Phenology in Relation to Springtime Meteorological Drivers. *Int. J. Biometeorol.* **56**(2): 343–355. doi:10.1007/s00484-011-0438-1. PMID:21557038.
- Lieth, H. 1974. Phenology and Seasonality modelling. Springer-Verlag, New York, NY, USA.
- Linsley-Noakes, G.C., Louw, M., and Allan, P. 1995. Estimating daily positive Utah chill units using daily maximum and minimum temperatures. *J. S. Afr. Soc. Hort. Sci.* **5**: 19–22. Available from <http://agris.fao.org/agris-search/search/display.do?f=1996/ZA/ZA96003.xml;ZA9500548> [accessed 1996].
- Lu, H., Raupach, M.R., McVicar, T.R., and Barrett, D.J. 2003. Decomposition of vegetation cover into woody and herbaceous components using AVHRR NDVI time series. *Remote Sens. Environ.* **86**: 1–18. doi:10.1016/S0034-4257(03)00054-3.
- Lüdeke, M.K.B., Badeck, F.-W., Otto, R.D., Häger, C., Dönges, S., Kindermann, J., Würth, G., Lang, T., Jäkel, U., Klaudius, A., Ramge, P., Habermehl, S., and Kohlmaier, G.H. 1994. The Frankfurt Biosphere Model: a global process oriented model of seasonal and long-term CO<sub>2</sub> exchange between terrestrial



- ecosystems and the atmosphere. I. Model description and illustrative results for cold deciduous and boreal forests. *Clim. Res.* 4: 143–166. Available from <http://www.int-res.com/articles/cr/4/c004p143.pdf> [accessed 25 August 1994].
- McMaster, G.S., and Wilhelm, W.W. 1997. Growing degree-days: one equation, two interpretations. *Agric. For. Meteorol.* 87(4): 291–300. doi:10.1016/S0168-1923(97)00027-0.
- Migliavacca, M., Cremonese, E., Colombo, R., Busetto, L., Galvagno, M., Ganis, L., Meroni, M., Pari, E., Rossini, M., Siniscalco, C., and Morra di Cella, U. 2008. European larch phenology in the Alps: can we grasp the role of ecological factors by combining field observations and inverse modelling? *Int. J. Biometeorol.* 52: 587–605. doi:10.1007/s00484-008-0152-9.
- Miller-Rushing, A.J., Katsuki, T., Primack, R.B., Ishii, Y., Lee, S.D., and Higuchi, H. 2007. Impact of global warming on a group of related species and their hybrids: cherry tree (*Rosaceae*) flowering at Mt. Takao, Japan. *Am. J. Bot.* 94: 1470–1478. doi:10.3732/ajb.94.9.1470.
- Morin, X., and Thuiller, W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, 90(5): 1301–1313. doi:10.1890/08-0134.1. PMID:19537550.
- Morin, X., Augspurger, C., and Chuine, I. 2007. Process-based modelling of tree species' distributions: what limits temperate tree species' range boundaries? *Ecology*, 88: 2280–2291. doi:10.1890/06-1591.1. PMID:17918406.
- Morin, X., Viner, D., and Chuine, I. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *J. Ecol.* 96: 784–794. doi:10.1111/j.1365-2745.2008.01369.x.
- Moser, L., Fonti, P., Büntgen, U., Esper, J., Luterbacher, J., Franzen, J., and Frank, D. 2010. Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. *Tree Physiol.* 30(2): 225–233. doi:10.1093/treephys/tpp108. PMID:20008326.
- Murray, M.B., Cannell, M.G.R., and Smith, R.I. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* 26: 693–700. doi:10.2307/2404093.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., and Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386: 698–702. doi:10.1038/386698a0.
- Nord, E.A., and Lynch, J.P. 2009. Plant phenology: a critical controller of soil resource acquisition. *J. Exp. Bot.* 60: 1927–1937. doi:10.1093/jxb/erp018. PMID:19286918.
- Ohlemüller, R., Gritti, E.S., Sykes, M.T., and Thomas, C.D. 2006. Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. *Glob. Ecol. Biogeogr.* 15(4): 395–405. doi:10.1111/j.1466-822X.2006.00245.x.
- O'Neill, B.F., Caffarra, A., Gleeson, E., Semmler, T., McGrath, R., and Donnelly, A. 2010. The use of climate projections in the modelling of bud burst. On poster programme CL2.4: Shifting Seasons: Phenological evidence from observations, reconstructions, measurements and models (co-sponsored by PAGES and ILEAPS). European Geosciences Union General Assembly, 2010, Vienna, Austria. Available from <http://www.tcd.ie/Botany/phenology/assets/Ensembles%20poster2.pdf>.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol.* 13: 1860–1872. doi:10.1111/j.1365-2486.2007.01404.x.
- Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(2): 37–42. doi:10.1038/nature01286. PMID:1251946.
- Peng, C., Guiot, J., Wu, H., Jiang, H., and Luo, Y. 2011. Integrating models with data in ecology and palaeoecology: advances towards a model-data fusion approach. *Ecol. Lett.* 14: 522–536. doi:10.1111/j.1461-0248.2011.01603.x. PMID:21366814.
- Peñuelas, J., and Filella, I. 2001. Phenology. Responses to a warming world. *Science*, 294: 793–795. doi:10.1126/science.1066860.
- Peñuelas, J., Rutishauser, T., and Filella, I. 2009. Ecology. Phenology feedbacks on climate change. *Science*, 324(5929): 887–888. doi:10.1126/science.1173004.
- Piao, S., Fan, J., Zhou, L., Ciais, P., and Zhu, B. 2006. Variations in satellite-derived phenology in China's temperate vegetation. *Global Change Biol.* 12: 672–685. doi:10.1111/j.1365-2486.2006.01123.x.
- Picard, G., Quegan, S., Delbart, N., Lomas, M.R., Le Toan, T., and Woodward, F.I. 2005. Bud-burst modelling in Siberia and its impact on quantifying the carbon budget. *Global Change Biol.* 11: 2164–2176. doi:10.1111/j.1365-2486.2005.01055.x.
- Post, E., and Pedersen, C. 2008. Opposing plant community responses to warming with and without herbivores. *Proc. Natl. Acad. Sci. U.S.A.* 105: 12353–12358. doi:10.1073/pnas.0802421105. PMID:18719116.
- Powell, L.E. 1987. Hormonal aspects of bud and seed dormancy in temperate-zone woody plants. *Hortscience*, 22: 845–850. <http://openagricola.nal.usda.gov/Record/IND87076835> [accessed 1988].
- Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., et al. 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Phil. Trans. R. Soc. B*, 365(1555): 3227–3246. doi:10.1098/rstb.2010.0102.
- Richardson, A.D., Anderson, R.S., Arain, M.A., Barr, A.G., Bohrer, G., Chen, G.S., et al. 2012. Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. *Global Change Biol.* 18(2): 66–584. doi:10.1111/j.1365-2486.2011.02562.x.
- Richardson, E.A., Seeley, S.D., and Walker, D.R. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience*, 9: 331–332.
- Rötzer, T. 2005. Climate change, stand structure and the growth of forest stands. *Ann. Meteorol.* 41(1): 40–43. Available from <http://www.wwk.forst.tu-muenchen.de/info/publications/OnlinePublications/591.pdf> [accessed 2005].
- Running, S.W., and Hunt, E.R. 1993. Generalization of a forest ecosystem process model for other biomes. BIOME-BGC, and an application of global-scale models. In *Physiological Processes, Leaf to Globe*. Edited by C. Field and J. Ehleringer. Academic Press Inc., New York. pp. 141–158.
- Schaber, J., and Badeck, F.W. 2003. Physiology - based phenology models for forest tree species in Germany. *Int. J. Biometeorol.* 47: 193–201. doi:10.1007/s00484-003-0171-5. PMID:12698325.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., and Mladenoff, D.J. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecol. Model.* 201: 409–419. doi:10.1016/j.ecolmodel.2006.10.009.
- Schwartz, M.D. 1990. Detecting the Onset of Spring: A Possible Application of Phenological models. *Clim. Res.* 1(1): 23–29. doi:10.3354/cr001023. Available from <http://www.int-res.com/articles/cr/1/c001p023.pdf> [accessed 1990].
- Schwartz, M.D. 1993. Assessing the Onset of Spring: A Climatological Perspective. *Phys. Geogr.* 14(6): 536–550. Available from [http://research.eeescience.utoledo.edu/lees/papers\\_PDF/Schwartz\\_1993\\_PhysGeogr.pdf](http://research.eeescience.utoledo.edu/lees/papers_PDF/Schwartz_1993_PhysGeogr.pdf) [accessed 1993].
- Schwartz, M.D. 1994. Monitoring global change with phenology: the case of the spring green wave. *Int. J. Biometeorol.* 38: 18–22. doi:10.1007/BF01241799.
- Schwartz, M.D. 1998. Green-wave Phenology. *Nature*, 394(6696): 839–840. doi:10.1038/29670, 10.1038/29667.
- Schwartz, M.D. 1999. Advancing to full bloom: planning phenological research for the 21st century. *Int. J. Biometeorol.* 42: 113–118. doi:10.1007/s004840050093.
- Schwartz, M.D., and Crawford, T.M. 2001. Detecting Energy-Balance Modifications at the Onset of Spring. *Phys. Geogr.* 21(5): 394–409. Available from [http://research.eeescience.utoledo.edu/lees/papers\\_PDF/Schwartz\\_2001\\_PhysGeogr.pdf](http://research.eeescience.utoledo.edu/lees/papers_PDF/Schwartz_2001_PhysGeogr.pdf) [accessed 2001].
- Schwartz, M.D., and Hanes, J.M. 2010a. Continental-scale phenology: warming and chilling. *Int. J. Climatol.* 30(11): 1595–1598. doi:10.1002/joc.2014.
- Schwartz, M.D., and Hanes, J.M. 2010b. Intercomparing Multiple Measures of the Onset of Spring in Eastern North America. *Int. J. Climatol.* 30(11): 1614–1626. doi:10.1002/joc.2008.
- Schwartz, M.D., and Reiter, B.E. 2000. Changes in North American Spring. *Int. J. Climatol.* 20(8): 929–932. doi:10.1002/1097-0088(20000630)20:8<929::AID-JOC557>3.0.CO;2-5.
- Schwartz, M.D., Reed, B.C., and White, M.A. 2002. Assessing Satellite-Derived Start-of-Season Measures in the Conterminous U.S.A. *Int. J. Climatol.* 22(14): 1793–1805. doi:10.1002/joc.819.
- Schwartz, M.D., Ahas, R., and Aasa, A. 2006. Onset of Spring Starting Earlier Across the Northern Hemisphere. *Global Change Biol.* 12(2): 343–351. doi:10.1111/j.1365-2486.2005.01097.x.
- Shaltout, A.D., and Unrath, C.R. 1983. Rest completion prediction model for Starkrimson Delicious apples. *J. Am. Soc. Hort. Sci.* 108: 957–961. Available from <http://openagricola.nal.usda.gov/Record/IND84001552> [accessed November 1983].
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., and Venevsky, S. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biol.* 9: 161–185. doi:10.1046/j.1365-2486.2003.00569.x.
- Snyder, R.L., Spano, D., Cesaraccio, C., and Duce, P. 1999. Determining degree-day thresholds from field observations. *Int. J. Biometeorol.* 42: 177–182. doi:10.1007/s004840050102.
- Sparks, T.H., Jeffree, E.P., and Jeffree, C.E. 2000. An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *Int. J. Biometeorol.* 44: 82–87. doi:10.1007/s004840000049. PMID:10993562.
- Storch, H., and Zwiers, F.W. 1999. Statistical analysis in climatology. Cambridge University Press, Cambridge. pp. 484.
- Steiner, A.L., Pal, J.S., Rauscher, S.A., Bell, J.B., Diffenbaugh, N.S., Boone, A., Sloan, L.C., and Giorgi, F. 2009. Land surface coupling in regional climate simulations of the West African monsoon. *Clim. Dyn.* 33: 869–892. doi:10.1007/s00382-009-0543-6.
- Strickler, K. 2007. Exploring Alternate Conceptions of Flowering Phenology with an Interactive Systems Model. In *Proceedings of the 9th International Conference: Pollination Symposium on Plant-Pollinator Relationships - Diversity in Action: Program and Abstracts*. Ames, IA, 24–27 June 2007. Edited by C.A.C. Gardener, M.A. Harris, R.W. Hellmich, et al. Iowa State University, Ames, IA, USA. pp. 212.

- Sung, S., and Amasino, R.M. 2004. Vernalization in *Arabidopsis thaliana* is mediated by the PHD finger protein VIN3. *Nature*, **427**: 159–164. doi:10.1038/nature02195. PMID:14712276.
- Thackery, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edward, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Smith, M., Smithers, R.J., Smithers, R.J., Winfield, I.J., and Wanless, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biol.* **16**(12): 3304–3313. doi:10.1111/j.1365-2486.2010.02165.x.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., and Grainger, A. 2004. Extinction risk from climate change. *Nature*, **427**(6970): 145–148. doi:10.1038/nature02121. PMID:14712274.
- Thuiller, W. 2007. Biodiversity: Climate change and the ecologist. *Nature*, **448**: 550–552. doi:10.1038/448550a. PMID:17671497.
- van Leeuwen, W., Casady, G., Neary, D., Bautista, S., Alloza, J., Carmel, J., Wittenberg, L., Malkinson, D., and Orr, B. 2010. Monitoring post-wildfire vegetation response with remotely sensed time series data in Spain, U.S.A. and Israel. *Int. J. Wildland Fire*, **19**: 75–93. doi:10.1071/WF08078.
- van Vliet, A.J.H. 2010. Societal Adaptation Options to Changes in Phenology. *Phenological Research*, 75–98. doi:10.1007/978-90-481-3335-2\_4.
- Visser, M.E., Caro, S.P., van Oers, K., Schaper, S.V., and Helm, B. 2010. Phenology, seasonal timing and circ-annual rhythms: towards a unified framework. *Phil. Trans. R. Soc. B*, **365**: 3113–3127. doi:10.1098/rstb.2010.0111.
- Vitasse, Y., François, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I., and Delzon, S. 2011. Assessing the effects of climate change on the phenology of European temperate trees. *Agric. For. Meteorol.* **151**(7): 969–980. doi:10.1016/j.agrformet.2011.03.003.
- Voigt, W., Perner, J., and Jones, T.H. 2007. Using functional groups to investigate community response to environmental changes: two grassland case studies. *Global Change Biol.* **13**: 1710–1721. doi:10.1111/j.1365-2486.2007.01398.x.
- White, M.A., and Nemani, R.R. 2003. Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest. *Global Change Biol.* **9**: 967–972. doi:10.1046/j.1365-2486.2003.00585.x.
- White, M.A., Nemani, R.R., Thornton, P.E., and Running, S.W. 2002. Satellite evidence of phenological differences between urbanized and rural areas of the eastern United States deciduous broadleaf forest. *Ecosystems*, **5**: 260–273. doi:10.1007/s10021-001-0070-8.
- Wilczek, A.M., Roe, J.L., Knapp, M.C., Cooper, M.D., Lopez-Gallego, C., Martin, L.J., Muir, C.D., Sim, S., Walker, A., Anderson, J., Egan, J.F., Moyers, B.T., Petipas, R., Giakountis, A., Charbit, E., Coupland, G., Welch, S.M., and Schmitt, J. 2009. Effects of Genetic Perturbation on Seasonal Life History Plasticity. *Science*, **323**(5916): 930–934. doi:10.1126/science.1165826. PMID:19150810.
- Wilczek, A.M., Burghardt, L.T., Cobb, A.R., Cooper, M.D., Welch, S.M., and Schmitt, J. 2010. Genetic and physiological bases for phenological responses to current and predicted climates. *Phil. Trans. R. Soc. B*, **365**: 3129–3147. doi:10.1098/rstb.2010.0128.
- Wilks, D.S. 1995. *Statistical methods in atmospheric sciences*. Academic Press, San Diego. pp. 467.
- Williams, J.W., and Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**: 475–482. doi:10.1890/070037.
- Winder, M., and Cloern, J.E. 2010. The annual cycles of phytoplankton biomass. *Phil. Trans. R. Soc. B*, **365**: 3215–3226. doi:10.1098/rstb.2010.0125.
- Wu, W., Shibasaki, R., Yang, P., Zhou, Q., and Tang, H. 2008. Variations in Cropland Phenology in China from 1983 to 2002. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*. Beijing. Vol. XXXVII. Part B7. Available from [http://www.isprs.org/proceedings/XXXVII/congress/7\\_pdf/10\\_ThS-18/02.pdf](http://www.isprs.org/proceedings/XXXVII/congress/7_pdf/10_ThS-18/02.pdf) [accessed 2008].
- Zhang, X., Friedl, M.A., and Schaaf, C.B. 2006. Global vegetation phenology from Moderate Resolution Imaging Spectroradiometer (MODIS): Evaluation of global patterns and comparison with in situ measurements. *J. Geophys. Res.* **111**: G04017. doi:10.1029/2006JG000217.
- Zhang, X., Friedl, M.A., Schaaf, C.B., Strahler, A.H., Hodges, J.C.F., Gao, F., Reed, B.C., and Huete, A. 2003. Monitoring vegetation phenology using MODIS. *Remote Sens. Environ.* **84**: 471–475. doi:10.1016/S0034-4257(02)00135-9.

## Appendix A

Table A1 appears on the following page.

**Table A1.** Key features and advantages of modeling and optimization techniques used in plant phenology models.

Modeling approaches	Features	Assumptions	PPMs	References	Advantages	Disadvantages
Statistical	Statistical fitting methods	HU, FU, PHU, HHU, etc.	TT, DD, SI, GDD, SW, PTT, HTT, etc.	McMaster and Wilhelm 1997; Wilks 1995; Storch and Zwiers 1999; Cannell and Smith 1983; Hunter and Lechowicz 1992; etc.	Literature widely available on subject; simplified calculation procedures; selecting the correct phenological or climatic mechanisms; simple and available temperature inputs; well-suited regions, species, and processes	Limited regions; small sets of events and plants; limited predictive ability
Mechanistic	Experimental approaches and statistical model-fitting techniques for known or assumed cause-effect relationships	FU, CU, CU+FU, WCU+CR	ForcSar, ForcTT, ST, Seq, Par, AT, DR, FP, UniForc, etc. Utah Model, North Carolina Model, Low Chilling Model, Positive Chill Unit Model, Chill Day Model, UniForc, etc.	Cannell and Smith 1983; Murray et al. 1989; Hänninen 1990, 1995; Kramer 1994; Chuine et al. 1999; Richardson et al. 1974; Gilreath and Buchanan 1981; Shaultout and Unrath 1983; Linsley-Noakes et al. 1995; Cesaraccio et al. 2002; etc.	Considering physical dimensions; incorporating the role of different growth-promoting factors, triggering events	Mechanism uncertainties; lacking a method for direct measurements of the state of development during physical processes
Theoretical	Cost-benefit tradeoff evolution relationships; satellite vegetation index (VI) data and methods for the optimization of model parameters	RPB (CB, HB), SFB (FB, NB, GB, etc.), RSB	BALANCE, DORMPHOT, FBM, Ecosys, CTEM, SILVAN, PIM, etc. GSI, SW	Lüdeke et al. 1994; Kikuzawa 1995; Kaduk and Heimann 1997; Grant et al. 1999; Chuine and Beaubien 2001; Bugmann 2001; Schaber and Badeck 2003; Arora and Boer 2005; Rötzer 2005; Strickler 2007; Scheller et al. 2007; O'Neill et al. 2010; etc.	Broad coverage; standardized response; multiple techniques integrated; flexible applications; realistic predictions; taking genetic or ecotypic variability into account when observations are available for different individuals or different populations of a species; allowing highlighting of processes involved in range shifts or extinctions; global coverage; integrated signal; etc.	Geographical variations in response; probable scale, technique-related confusions, etc.; restricted species and scales; unsuitable predictions under novel climate changes, etc.; short period-of-record; cloud cover interference; interpretation issues; small set of measures, etc.

**Note:** HU, heat unit; TT, thermal time; DD, degree day; SI, spring index; GDD, grown degree day; SW, spring warming; PHU, photo-heat unit; HHU, hydro-heat unit; PTT, photo-thermal time; HTT, heat-thermal time; FU, forcing units; CU, chilling unit; CR, chilling requirement; WCU, weighted chilling unit; ForcSar, forcing sarvas; ForcTT, forcing thermal time; ST, sequential time; Seq, sequential; Par, parallel; AT, alternating; DR, deepening rest; FP, four phase; UniForc, unified forcing; RPB, reproductive fitness-based processes; CB, carbon balance based; HB, hormone actions and interactions based; SFB, survival fitness-based processes genetic behavior; FB, fitness based; NB, niche based; GB, genetic behavior based; FBM, the Frankfurt Biosphere Model by Lüdeke et al. (1994); Ecosys, the ecosystem model by Grant et al. (1999); CTEM, the Canadian Terrestrial Ecosystem Model; PIM, promoter-inhibitor Model; RSB, remote sensing based; GSI, growing season index; SW, spring warming.