Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central Europe

David Basler*

Institute of Botany, University of Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland

A B S T R A C T

Inter-annual variation in climate is reflected by changes in the timing of phenology. Over the last decades a considerable number of models have been developed in order to explain the inter-annual variation of spring phenology in trees. Contrary to empirical models, "process-based" models aim at simulating physiological processes in order to yield more realistic predictions of growing season onset dates. Despite the increasing knowledge on the environmental controls of seasonal dormancy in trees, the detailed action and interaction of the involved environmental drivers (chilling, photoperiod and warm temperature) remains to be elucidated. This study aims at a uniform comparison of a wide range of existing models (and new recombinations), on a multitude of long-term observation series in six tree species across central Europe, using extensive cross-validation. Even though the assessed models differ in the phases of dormancy and environmental drivers accounted for, they yielded a surprisingly similar quality of prediction of leaf unfolding dates. Depending on the species, the lowest average prediction errors for leaf unfolding (*RMSE*) ranged from 7 to 9 days for the dataset pooled across sites and years and from 4 to 6 days for site-specific predictions, in absence of any obvious geographical pattern. Simple models, that feature ecodormancy release only, performed similar or better than more complex models, which additionally include endodormancy release through chilling temperatures. Model parameterisation tended to converge towards similar behaviour and models with many parameters tended to overfit on the 40 year time-series of leaf unfolding. Additionally, all models tended to underestimate the inter-annual variation of leaf unfolding and failed to predict very early or late dates of leaf unfolding in certain years. The transfer of site-specific parameters to other sites was associated with an almost doubling of the average prediction error, independent of distance and climatic similarity between the calibration and validation sites. The findings challenge the accurate implementation of the physiological processes controlling spring phenology in the models and highlight shortcomings associated with model parameterisation on observational time-series only.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Plant phenology studies the seasonal and visible phenomena of plant development related to weather. The timing of phenological events reflects a combination of internal (genetic) settings and environmental influences. Given its significance for avoiding late spring freezing damage and impacts of early autumnal cold events, a well-timed phenology is crucial for plant survival. In addition, the control of synchronous flowering among individuals assures sexual reproduction. The phenological events defining the onset and end of the growing season are of special interest, since they are setting the length of the growing season, and

thereby controlling range limits of species (Chuine and Beaubien, 2001). During the dormant period, buds pass through three distinct states of dormancy (Lang et al., 1987): (1) paradormancy, a state of specific bud dormancy maintained due to physiological factors outside the bud but inside the plant (e.g., apical dominance), (2) endodormancy, state of inactivity mediated by factor inside the bud and (3) ecodormancy, a state of inactivity imposed by unfavourable environmental conditions at otherwise full preparedness for advancing seasonal development. The transitions between the different phases of dormancy are gradual and species-specific (Perry, 1971). In tree species adapted to cool climates, dormancy is induced by the shortening of day-length in autumn, perceived in leaves, and modulated by concurrent temperatures. Moderate sub-zero temperatures are then inducing endodormancy, which is generally released in late winter or early spring, after sufficiently long exposure to cool, but non-freezing temperatures in

* Tel.: +41 61 267 35 11; fax: +41 61 267 35 04.
  E-mail address: david.basler@unibas.ch

the range of 2–7 °C ("chilling"; Coville, 1920; Doorenbos, 1953; Battey, 2000). Many species need an additional weather independent photoperiod signal to effectively advance the transition from endodormancy to the following ecodormancy. During this stage, actual weather (largely temperature) controls bud development and bud burst (environmental "forcing").

Phenology gained much attention during the last decades, once its implications in the climate change discussion became acknowledged. Ever since phenological data was collected, the phenological events were related to climate and simple models were built to calculate the timing of phenological phases, especially in agroecosystems. Nowadays, the applications of phenological models range from reconstruction and quality assessment of phenological time-series, spatial extrapolation of observations and even to species-specific predictions of phenology, and thus species performance, in future climate. Thus, phenology plays an important role in species distribution models (e.g., Chuine and Beaubien, 2001) or dynamic global vegetation models (e.g., Krinner et al., 2005). Through the intimate linkage with the length of the growing season and thus, net primary production, phenology plays also an important role in carbon cycle models at ecosystem and global scale (Richardson et al., 2013). For temperate and boreal tree species, numerous models have been developed to simulate the events of spring phenology, such as bud burst or leaf unfolding, whereas only few models attempted to simulate the autumnal phases of phenology, such as leaf colouration and leaf fall (White et al., 1997; Delpierre et al., 2009). The more mechanistic models commonly outperform simple correlative statistical models for phenology, which often use linear correlations to spring temperature only (but see Olsson and Jönsson, 2014). These "process-based" models are also able to reflect the non-linear responses of phenology to the various environmental drivers. In simple phenological models, the bud development towards bud-burst is basically defined as a response to concurrent temperature, mostly by adopting the concept of accumulated temperature over a certain threshold (degree days). However, the shortcomings of this simple approach (accounting for the release of ecodormancy only) and the increasing knowledge of the underlying physiological processes motivated the development of numerous advanced models for spring phenology, which account also for chilling and photoperiod influences. Most recently, even the complex interactions of all three drivers of spring phenology, chilling signals, photoperiod, and actual thermal forcing were integrated into a single model (Caffarra et al., 2011). However, with the increasing number of factors, complexity of models increases dramatically and parameterisation becomes increasingly difficult. At first, the statistical fitting of parameters was difficult and often led to unstable parameter estimates (Kramer, 1994), thus Hänninen (1995) compared 96 model formulations using parameters derived from literature. Later, efficient optimisation methods (Chuine et al., 1998) and appropriate methods for the statistical estimation of prediction errors, such as bootstrapping (Häkkinen, 1999) or cross-validation (Chuine et al., 1999) led to further improvement of model parameterisation and evaluation. No single model structure was found to predict spring phenology across different species, so the best predictive models are still species-specific (Hunter and Lechowicz, 1992; Chuine et al., 1998; Schaber and Badeck, 2003) and different model structures may perform equally well for a given species (Schaber and Badeck, 2003). A recent uncertainty analysis for a set of phenological models using data from Harvard forest revealed, that prediction errors are largely a result of the uncertain nature and strength of the actual drivers (model structure), and to a lesser extent due to model parameterisation (Migliavacca et al., 2012). The more recently developed models have been tested on rather limited datasets for only a few species. The current study collectively analyses the performance of current process-based phenology model structures for three aspects (1) generalisation, (2)

site-specific accuracy and (3) spatial transferability, using a large and consistent phenology data set covering 40 year of observation on a multitude of sites throughout Europe for 6 temperate tree species. The assessed models differ with respect to the mechanisms they account for (dormancy induction, endodormancy release and ecodormancy release), the employed drivers (forcing temperature, chilling temperature and photoperiod), and the specific responses for different species. This study aims at improving the understanding of the capabilities and uncertainties of these models, and disclosing some pitfalls in modelling the spring phenology of temperate and boreal forest trees.

2. Material and methods

2.1. Models types

The "process-based" phenology-models published so far, and included here, simulate the environmental influence on bud development, until a critical developmental threshold for bud burst or leaf unfolding is reached. Parameters common to most models are a starting date, after which the specific environmental drivers affect bud development, and one or more parameters controlling the rate of response to environmental drivers.

The models are grouped according to their scope of operation into three categories: (1) models explaining ecodormancy release only, (2) models explaining the release of endo- and ecodormancy and (3) models explaining the whole transition from dormancy induction until bud burst. Further, I classified models by the environmental drivers they are accounting for: chilling temperature, photoperiod and forcing temperature (Table 1). Models were implemented according to the original publication (Table 1, supplementary Table S1); however, I fitted the starting date rather than using an arbitrary date (such as 1 January). For each parameter, upper and lower limit was defined within a wide, but (biologically) reasonable range (see supplementary Table S2).

2.1.1. Models accounting for ecodormancy release only.

These are the oldest models, dating back to de Réaumur (1735), accounting for thermal forcing in spring only. These "Thermal Time" models (Wang, 1960; Cannell and Smith, 1983; Hunter and Lechowicz, 1992; Chuine et al., 1999) are using degree days as forcing units. A modification of this model type, hereafter named the "sigmoid Thermal Time model" (Hänninen, 1990; Kramer, 1994) uses a sigmoid, rather than linear, forcing function (see supplementary Table S1). Although photoperiod is well known to influence phenology of crops (e.g., Masle et al., 1989; Siebert and Ewert, 2012) and late successional tree species (Caffarra and Donnelly, 2010; Körner and Basler, 2010; Basler and Körner, 2014), few models yet include photoperiod as explicit driver of spring phenology (the fixed starting date of most models may, however, imply a strong photoperiod threshold). In the Photothermal-time model developed for crops (Masle et al., 1989) and successfully applied to trees by Črepinšek et al. (2006), photoperiod has been included as an additional factor influencing the rate of forcing. Recently, a study investigating the shortcomings of the classic Thermal Time model again suggested the inclusion of photoperiod as explicit driver and thereby proposed an extension of the Photothermal-time model by an additional exponential constant (M1 model; Blümel and Chmielewski, 2012).

2.1.2. Models accounting for endo- and ecodormancy release.

The chilling requirement, indicating to the plant that winter has passed, plays an additional role in dormancy release of temperate and boreal trees. In current models, the response to chilling temperatures is implemented either as a triangular function of temperature (defined by minimal chilling temperature, optimal chilling