

Performance of tree phenology models along a bioclimatic gradient in Sweden



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ABSTRACT

Tree phenology has been recognized as an important indicator of climate change, and a wide range of budburst models have been developed. The models differ in temperature sensitivity, and the choice of model can therefore influence the result of climate impact assessments. In this study we compared the ability of 15 models to simulate budburst of the main forest tree species in Sweden. Records on the timing of budburst, available for 1873–1918 and 1966–2011, were used for model evaluation. The predefined models, having different chilling, competence and forcing modules, represented different hypothesis on temperature impact on tree phenology. We extracted the model-specific forcing units accumulated by the observed day of budburst, and tested for covariation with bio-climatic gradients. For all tree species, most models indicated a negative relation between forcing requirement and latitude, which may indicate provenance specific adaptations. The thermal continentality index, which in Sweden is highly correlated with latitude, did provide some additional explanation for the period of 1873–1918 but not for the period of 1966–2011. For most model- and tree species combinations, temperature anomalies explain a significant part of the variability in forcing units accumulated at day of budburst. This indicates that the budburst models were not able to fully track the response to inter-annual variations in temperature conditions, probably due to difficulties in capturing species and provenance specific chilling requirement, day length response and impact of spring backlashes.

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1. Introduction

Plant phenology is influenced by temperature, and has been recognized as an important indicator of climate change (Menzel et al., 2006). Europe and North America have been experiencing a lengthening of the growing season since 1950s, due to earlier springs and later autumns (Menzel and Fabian, 1999; Ahas et al., 2002; Menzel and Sparks, 2006; Menzel et al., 2008). The trend is more pronounced at high latitudes than further south (White et al., 1999). The temperature response is however species-specific, and tree species growing in the same region may respond differently. The growing season may for instance become longer for *Fagus sylvatica* but shorter for *Quercus robur* in a warmer climate, due to differences in leaf senescence (Kramer, 1995). Many boreal and temperate tree species require a chilling period with cold temperatures to break winter rest, before warm forcing temperatures can trigger budburst (Cannell and Smith, 1986). The chilling requirement is an

adaptation to prevent early onset of growth, minimizing the risk of frost damage due to spring backlashes (Cannell and Smith, 1983). The length of the growing season influences the biochemical cycles of nitrogen, carbon and water (Ibáñez et al., 2010), thereby affecting the productivity of terrestrial ecosystems (Rotzer et al., 2004; Noormets et al., 2009).

The performance of ecosystem models simulating plant–atmosphere interaction and ecosystem productivity are enhanced by accurate predictions of phenological events (White et al., 1999; Leinonen and Kramer, 2002; Rotzer et al., 2004; Kucharik et al., 2006; Jeong et al., 2012; Migliavacca et al., 2012; Richardson et al., 2012). Tree phenology is also important when modeling species distribution, as it can affect survival and reproductive success (Chuine and Beaubien, 2001). A perfect model should have high accuracy, high generality and high reality; qualities that are difficult to combine (Levins, 1968). A wide range of different phenology models have been presented including empirical models, intermediate empirical models and process-based models (Vegis, 1964; Cannell and Smith, 1983; Kobayashi and Fuchigami, 1983; Hänninen, 1990; Hunter and Lechowicz, 1992; Chuine, 2000; Schaber and Badeck, 2003; Caffarra et al., 2011). The model structure is of main importance for its temperature

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response (Migliavacca et al., 2012). An empirical site-specific phenology model may have higher accuracy than a more general and process-based model, but it is less suitable for the extrapolation needed in climate change impact assessments (Trivedi et al., 2008).

The winter dormancy of boreal and nemo-boreal tree species are commonly activated by short days and cold nights, and reversed by longer days and warm temperatures. The effect of temperature and photoperiod can be interactive, and long days may compensate for incomplete chilling (Kramer, 1995; Myking and Heide, 1995). Provenance specific adaptations created by natural selection on phenological properties can be observed along bioclimatic gradients, such as the latitudinal gradient and the degree of continentality (Langlet, 1960; Hannerz, 1994). For example, southern Norway spruce provenances generally have higher forcing requirements than northern provenances, which is an adaptation to slower seasonal transitions and higher risk of spring backlash in central and eastern Europe compared with northern Europe which mean that two provenances planted on the same site will burst bud at different times (Hannerz, 1994). The impact of environmental factors such as water and nutrient availability, is acknowledged but less understood, as most research has focused on temperature and photoperiod (Hudson, 2010). Bud setting and leaf senescence provides visible signs of ongoing phenological processes, whereas biochemical adjustments associated with frost tolerance (Körner, 2006) are not easily observed. This, in combination with species-specific adaptations, has led to the development of a variety of modeling concepts, reflecting the difficulties in quantifying plant responses to temperature conditions.

The objective of this study is to compare the ability of 15 models to simulate budburst of five common forest tree species in Sweden (*Picea abies*, *Pinus sylvestris*, *F. sylvatica*, *Betula* spp. and *Q. robur*). The models were selected to include common model concepts for forcing and chilling in the analysis, while varying in model complexity. Field observations were used to assess the performance of 1 photoperiod model, 3 forcing models, 1 photoperiod-forcing model, 8 chilling-forcing models, 1 chilling-photoperiod-forcing model and 1 hormone model. The models describe different hypothesis on temperature and day length impact on tree phenology, and we explore the models behavior in relation to the different species. Specifically, we asked (i) if the model specific forcing states at the timing of observed budburst correlated with latitude, indicating provenance specific adaptation. We also asked whether (ii) the thermal continentality index (TCI) or (iii) inter-annual temperature deviations could provide any explanation in addition to the latitude. Finally, we propose (iv) a model evaluation procedure for selecting models for climate change impact assessments.

2. Materials and methods

2.1. Winter dormancy and spring phenology

The selected budburst models simulate the phases of ontogenetic development, using temperature- and photoperiod thresholds in combination with temperature sums (Fig. 1). Two stages of dormancy can be recognized: endodormancy when the bud development is inhibited by internal factors of the bud, and ecodormancy during which the bud remains dormant as long as the temperature conditions are unfavorable for growth (Vegis, 1964; Kobayashi and Fuchigami, 1983; Horvath et al., 2003). Some models focus on ecodormancy only, whereas others also include endodormancy.

The state of dormancy is commonly modeled by linear or logistic functions, expressing the daily accumulation of chilling and forcing temperatures. Endodormancy has been related both to the number of chilling days, and to the accumulation of chilling

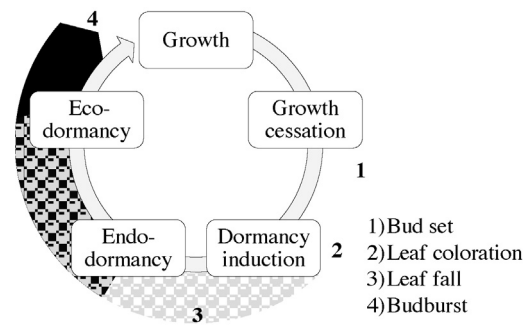


Fig. 1. A conceptual graph of temperature driven budburst models: the phenological phases, shown by boxes, may overlap and the timing of phenological events, like those of a deciduous tree (1–4), are influenced by both genetic properties and environmental conditions. All models included in the study have a forcing module (black), and some of them also have a chilling module (gray dots on white). Depending on the competence module (Fig. 2), the transition zone (gray dots on black) will either be described as a switch from chilling to forcing, or account for parallel chilling and forcing.

units (CU) with the rate of chilling being influenced by daily mean temperature. The chilling status determines the bud's ability to respond to forcing temperatures (Hänninen, 1990), and the chilling and forcing modules are commonly linked via the bud's competence (K). In some models, the competence is described by photoperiod instead of chilling. Forcing units (FU) will not start to accumulate until the competence is above zero (Fig. 2). Budburst is modeled to occur when a critical amount of forcing temperature has accumulated (FU_{crit}). The FU_{crit} is mostly fixed (Hänninen, 1990), but a few models have included a dynamic description with FU_{crit} being exponentially reduced by the length of chilling exposure ($T < 5^\circ\text{C}$) (Cannell and Smith, 1983).

Chilling, competence and forcing modules can be used in different combinations (see Hänninen, 1995; Chuine et al., 1999; Richardson and O'Keefe, 2009). In this study, we use 15 pre-defined models (Table 1, Fig. 3): 1 photoperiod model (M1), 3 forcing models (M2, M9 and M13), 8 chilling-forcing models (M3–M8, M10 and M11), 1 photoperiod-chilling forcing-model (M12), 1 photoperiod-forcing model (M14) and 1 hormone model (M15). Detailed model descriptions are provided as supplementary material. The

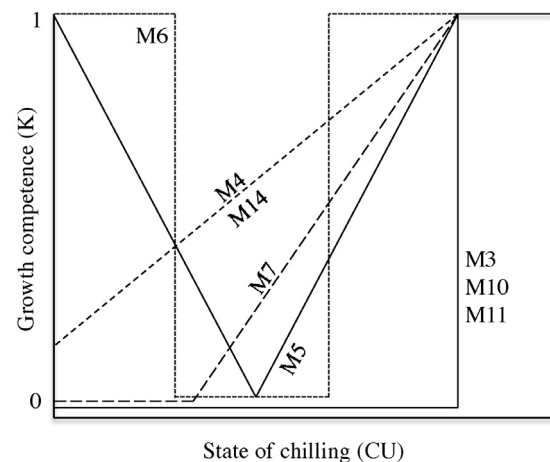


Fig. 2. The growth competence is a function of the model-specific accumulation of chilling, and the current state of competence regulates the daily accumulation of forcing units. M3, M10 and M11 are sequential, implying that a certain amount of chilling is required before forcing can start to accumulate. In M4–M7 and M14, chilling and forcing accumulate in parallel. In general, the forcing becomes more efficient as more chilling accumulates. M7 requires a small amount of chilling before forcing can start to accumulate, whereas M5 and M6 first experience a decrease in competence and then an increase in response to chilling accumulation.

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