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Understanding the environmental regulation of tree phenology

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DEPARTMENT OF PHYSICAL GEOGRAPHY AND ECOSYSTEM SCIENCE | LUND UNIVERSITY

Understanding the environmental regulation of tree phenology

Tetiana Svystun

DOCTORAL DISSERTATION

by due permission of the Faculty of Science, Lund University, Sweden.
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Abstract

In temperate and boreal climates, trees synchronise their annual growth cycles with seasonal changes in daylength and temperature. Understanding how environmental cues regulate tree phenology is important to our ability to capture the potential responses of trees to climate change, with implications for forest productivity.

In this thesis, we demonstrated that different research methods can be applied to study the regulation of tree phenology and that this knowledge can be used to generate climate change impact assessments. The knowledge gaps identified by summarising recent advances on the molecular regulation of growth cessation and bud set were addressed by modelling. Modelling autumnal bud development showed that both photoperiod and temperature help to predict the timing of bud set in non-stressful conditions, while additional regulatory mechanisms may be involved under stressful conditions.

The differences in phenological response to environmental signals between populations and provenances were accounted for via the values of model parameters. The provenance specific temperature sum requirements for bud burst for Norway spruce were used to calculate the risk of spring frost damage under current climate conditions and future climate scenario. The timing of bud burst will occur earlier in future and will be associated with an increased risk of spring frost damage due to the increased frequency and severity of spring frost events. The information on the provenance specific frost risk will facilitate forest management decisions on choosing suitable plant material for regeneration.

The ecosystem model was used to assess the effect of phenology parameterisation on simulating carbon uptake. Model simulations with calibrated phenology parameterization predicted enhanced forest productivity by the end of the century due to earlier timing of bud burst. However, uncertainty remains whether reduced winter chilling may slow down future bud burst advancement and forest productivity increase, highlighting the need for a mechanistic understanding of environmental regulation of dormancy release and bud burst.

Further progress towards a better understanding of regulation of tree phenology can be achieved through integrating molecular and modelling approaches, by incorporating knowledge on molecular pathways of environmental control of stages of the annual growth cycle into phenological models.

Key words: phenological events, environmental cues, temperature response, phenological modelling, frost risk, gross primary production, climate change impact

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Singh, R. K., **Svystun, T.**, AlDahmash B., Jönsson, A.M. and Bhalerao, R.P.
New Phytologist, 213, 511-524 (2017)

II **Modelling *Populus* autumn phenology: The importance of temperature and photoperiod**
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III **Model analysis of temperature impact on the Norway spruce provenance specific bud burst and associated risk of frost damage**
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Forest Ecology and Management, 493, 119252 (2021)

IV **Modelling *Populus* phenological response to climate change**
Svystun, T., Jönsson, A.M.
Submitted (2021)

Author contributions

Paper I	TS prepared the first draft of the manuscript and participated in the writing of the final version of the manuscript.
Paper II	TS was responsible for the study design, performed the simulations and analysis, and led the writing of the manuscript. All authors contributed to the manuscript.
Paper III	TS performed the simulations and analysis, and led the writing of the manuscript. All authors contributed to the manuscript.
Paper IV	Both authors contributed to the study design. TS performed the simulations and analysis, and led the writing of the manuscript.

Abstract

In temperate and boreal climates, trees synchronise their annual growth cycles with seasonal changes in daylength and temperature. Understanding how environmental cues regulate tree phenology is important to our ability to capture the potential responses of trees to climate change, with implications for forest productivity.

In this thesis, we demonstrated that different research methods can be applied to study the regulation of tree phenology and that this knowledge can be used to generate climate change impact assessments. The knowledge gaps identified by summarising recent advances on the molecular regulation of growth cessation and bud set were addressed by modelling. Modelling autumnal bud development showed that both photoperiod and temperature help to predict the timing of bud set in non-stressful conditions, while additional regulatory mechanisms may be involved under stressful conditions.

The differences in phenological response to environmental signals between populations and provenances were accounted for via the values of model parameters. The provenance specific temperature sum requirements for bud burst for Norway spruce were used to calculate the risk of spring frost damage under current climate conditions and future climate scenario. The timing of bud burst will occur earlier in future and will be associated with an increased risk of spring frost damage due to the increased frequency and severity of spring frost events. The information on the provenance specific frost risk will facilitate forest management decisions on choosing suitable plant material for regeneration.

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Further progress towards a better understanding of regulation of tree phenology can be achieved through integrating molecular and modelling approaches, by incorporating

knowledge on molecular pathways of environmental control of stages of the annual growth cycle into phenological models.

Introduction

Environmental regulation of annual growth cycle

In temperate and boreal climates, trees undergo alternating periods of active growth and growth arrest or dormancy throughout the year, hereafter referred to as annual growth cycles. The developmental stages of annual growth cycles (Fig. 1) are characterised by significant morphological, biophysical and physiological changes (Druart et al., 2007). The timing of these stages, phenology, is synchronised with seasonal changes in two main environmental cues, daylength and temperature (Cooke et al., 2012; Hänninen, 2016; Petterle et al., 2013). Understanding the environmental regulation of tree phenology is important for understanding the potential responses of trees to climate change, with implications for forest productivity.

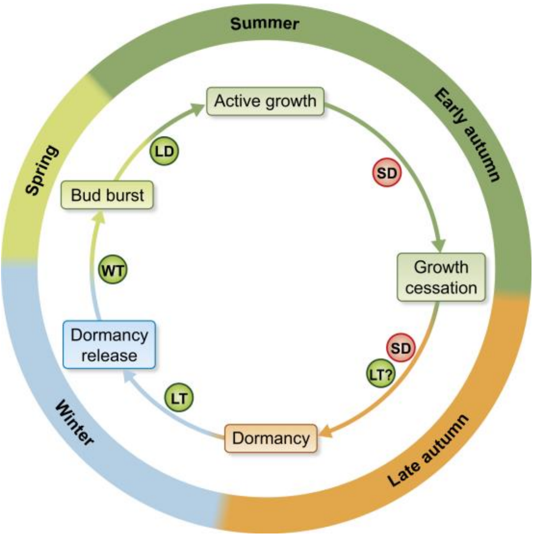

Figure 1.
Annual growth cycle in trees. Reduction in daylength (short days, SD) during late summer/early autumn induces the cessation of growth and bud set in trees such as poplar and spruce. Prolonged exposure to SDs in late autumn induces the establishment of dormancy in buds. In a dormant state, meristem and perennating organs, such as leaf primordia, become insensitive to growth-promotive signals. Low non-lethal temperatures progressively lead to dormancy release, following which growth arrest is primarily maintained by low temperatures in the winter. After release from dormancy, 'warm' temperatures (a few degrees higher than the dormancy-releasing temperature) in the spring promote bud burst in species such as poplar. In species such as birch and apple, low temperature induces both dormancy establishment and release, and promotes bud burst. LD, long days; LT, low temperature; WT, warm temperature. Reproduced from Paper I.

Growth cessation and bud set

The seasonal reduction in photoperiod (short days) plays a major role in regulating the transition from active growth to dormancy, as it is a more reliable cue of seasonal change than temperature (Rinne et al., 2010). When photoperiod drops below a growth-permitting value (critical daylength) the cessation of apical elongation growth and initiation of bud formation occur (Kayal et al., 2011; Petterle et al., 2013; Ruttink et al., 2007). As cell division and elongation are gradually suspended, young leaf primordia develop into embryonic leaves and bud scales, within which the internodes of embryonic shoots emerge and expand. The completion of internodes elongation results in the formation of a closed bud (bud set) (Cooke et al., 2012; Rohde and Boerjan, 2001; Ruttink et al., 2007). A number of studies provided evidence for the role of temperature in modulating the photoperiodic regulation of growth cessation and bud set, with both accelerated and delayed effects on bud set being observed (Howe et al., 2000; Junttila et al., 2003; Kalcsits et al., 2009; Mølmann et al., 2005).

Leaf senescence

The growth cessation and bud set are the prerequisites for leaf senescence, which is most likely induced by a light-dependent factor independently of temperature, while the speed of senescence has been shown to depend on temperature (Bhalerao et al., 2003; Fracheboud et al., 2009; Keskitalo et al., 2005; Michelson et al., 2018). During senescence, the chloroplast breakdown is accompanied by substantial functional metabolic changes, including replacement of carbon assimilation by the degradation of chlorophyll and leaf constituents, such as various macromolecules, protein complexes and membrane lipids. The liberated mineral nutrients and nitrogenous products are exported from the senescing leaves to the stem, where they are converted to storage forms. The completion of remobilization leads to the formation of an abscission and separation layer in the petiole, and to leaf abscission (Fracheboud et al., 2009; Keskitalo et al., 2005).

Dormancy establishment

There is a sparse understanding of the regulation of dormancy, i.e. the state at which meristem and perennating organs, such as leaf primordia, become insensitive to growth-promotive signals (Rohde and Bhalerao, 2007). Whether short days or low temperature are involved in dormancy establishment remains uncertain (Baba et al., 2011). It has been hypothesised that dormancy establishment can be induced by symplastic isolation of shoot apical meristem from the shoot system by blockage of phloem tubes with callose and protein-containing dormancy sphincter complexes (Rinne and Schoot, 2003; Rinne et al., 2011). However, this phenomenon could simply be non-causally correlated with dormancy development.

Dormancy release and bud burst

The dormancy release and bud burst are mainly regulated by temperature, while the effect of photoperiod has also been suggested. Prolonged exposure to low temperatures (chilling) is needed to release from dormancy, which, according to the hypothesis of symplastic isolation of shoot apical meristem, may be related to the upregulation of the expression of enzymes, which degrade callose plugs, enabling meristem to respond to growth promotive signals (Levy et al., 2007). Additional exposure to warm temperatures in spring (forcing) leads to reactivation of growth, accompanied by internode elongation and bud burst (Rinne et al., 2011). Insufficient chilling may lead to increased forcing requirement and delayed bud burst, this may however be compensated by long photoperiods (Hannerz et al., 2003; Man et al., 2017). On the other hand, short photoperiod prevents premature bud development before winter solstice (Heide, 1993; Myking and Heide, 1995).

Molecular approach

In recent years, understanding of the molecular mechanism involved in the seasonal regulation of growth in trees has been substantially improved, mostly by using *Populus* as a perennial plant model system. It is easy to transform, and genome sequence and resources for genomic and genetic analyses of *Populus* trees are available (Ellis et al., 2010). The molecular data of high temporal resolution, including seasonal patterns of gene expression, epigenetic modifications, and quantities of proteins, metabolites and other molecules, can be obtained and analysed in relation to the developmental process (Kudoh, 2016). The key advances include elucidation of the molecular components of the photoperiodic pathway of growth control (Azeez et al., 2014; Karlberg et al., 2010; Randall et al., 2015; Tylewicz et al., 2015) and molecular basis of a latitudinal cline in the timing of bud set (Böhlenius et al., 2006).

Modelling tree phenology

The environmental regulation of the timing of developmental stages of the annual growth cycle is often studied by means of phenological models. Two main concepts for modelling growth cessation and bud set have been described. The most recognized one is the regulation of growth cessation by the perception of the environmental signal, i.e. occurrence of the critical daylength (Ekberg et al., 1979; Heide, 1974). The second is the joint effect of daylength and temperature, according to which increased temperature sum accumulation during the growing season accelerates cessation of growth (Koski and Sievanen, 1985). However, other interactive influences of temperature on growth cessation and bud set have been suggested.

Autumn senescence is commonly modelled as a function of temperature accumulation below a threshold value, with the effect being modified (increased or decreased) by daylength. In further modifications, the growing season components are considered, such as bud burst, growing season mean temperature and growing season precipitation (Zani et al., 2020).

Several concepts for modelling dormancy release and bud burst have been established (Hannerz, 1999). The simplest one is based on the forcing requirement for bud burst, others involve chilling and forcing requirements (occurring sequentially or in parallel) and may also include photoperiod (as a starting day for forcing accumulation, or as a dynamic variable modifying the temperature response) (Hänninen, 1995; Linkosalo et al., 2008; Partanen et al., 2001). The sequential approach assumes fixed chilling and forcing requirements for bud burst, and fulfilment of the chilling requirement prior to start of forcing accumulation. The temperature sum model can be considered as a simplification of the sequential model. In the parallel approach, the requirements are not fixed, and the forcing requirement or the rate at which forcing accumulates depends on the amount of accumulated chilling (Linkosalo et al., 2006; Linkosalo et al., 2008).

Climate change impact

The impact of climate change on the timing of the developmental stages of the annual growth cycle will depend on the environmental factors regulating the transitions between the stages (Way, 2011). The growth cessation and bud set have been suggested to be less responsive since their timing is mainly regulated by photoperiod (Ingvarsson and Bernhardsson, 2020), although the interactive effect of temperature on photoperiodic control of growth may modify the response. The leaf senescence phenology demonstrated different types of response to temperature increase, indicating that while being initiated by a light-dependent factor, other actors, e.g. precipitation, solar radiation and photosynthetic capacity of the tree, may alter the response (Gill et al., 2015). The earlier timing of bud burst is expected in a warmer climate (Fu et al., 2014; Menzel et al., 2006), and it may be associated with an increased risk of spring frost damage due to a higher frequency of spring backlashes (Jönsson and Bärring, 2011). However, reduced accumulation of chilling due to warmer winters may slow down the rate of bud burst advancement, thereby decreasing the risk of spring frost damage (Fu et al., 2015; Laube et al., 2014). The shifts in the timing of phenological events will also influence the carbon uptake by trees (Keenan et al., 2014; Piao et al., 2007; Richardson et al., 2013). In this respect, the climate change impact on tree phenology and forest productivity can be addressed by scenario assessments, carried out by the ecosystem models.

Aims and objectives

The main objectives of the research presented in this thesis were to improve our understanding of how environmental factors regulate the timing, phenology, of key developmental stages of the annual growth cycle of trees in temperate and boreal regions, and to use this knowledge to generate climate change impact assessments, including potential changes in tree phenology and implications for forest productivity. The specific aims were to:

- Summarise current understanding of the mechanisms involved in seasonal regulation of growth with a molecular perspective and identify key issues to be addressed by means of modelling (Paper I).
- Investigate the role of photoperiod and temperature in autumnal bud development by evaluating different models that based on either only photoperiod or both climatic factors (Paper II).
- Analyse the provenance specific timing of bud burst and associated risk of frost damage under current climate conditions and future climate scenario (Paper III).
- Assess the changes in spring and autumn phenology and corresponding changes in carbon uptake by deciduous trees in response to the ongoing climate change (Paper IV).

Material and method

Literature review

The process of conducting a review paper involves several steps to be taken, such as formulating the research objectives, identifying relevant literature, abstracting appropriate information from each literature source, synthesising existing knowledge across the published literature, and providing insights into novel areas for new research (Snyder, 2019). (Snyder, 2019). In Paper I, we summarised current knowledge of the cellular and molecular mechanisms that control developmental transitions at the terminal bud from active growth through growth cessation, dormancy establishment and dormancy release in trees in temperate and boreal regions. We selected the peer-reviewed publications focusing mainly on *Populus* species since the majority of molecular studies have been carried out in *Populus*, and two environmental factors, photoperiod and temperature. However, key molecular studies on other species were also included. In the review, the knowledge gaps remaining to be explored were identified, and hypothesis and future perspective were discussed.

Phenological data

Penological data on two species important in Swedish forestry, European aspen *(Populus tremula)* and Norway spruce *(Picea abies)*, were used in Papers II-IV (Table 1).

Table 1.
Summary of the datasets used in the thesis.

Paper	Phenological data				Climate data		
	Provider	Specie	Phase/ assessment	Period	Name/ Provider	Variable	Period
II	Umeå Plant Science Centre	European aspen	Bud set (field)	2005-2007	Station SMHI	Temperature Precipitation	2006-2015
		European aspen	Photoperiod at bud set (growth chamber)	-			
		Hybrid aspen	Bud formation (greenhouse)	-			
III	Skogsforsk	Norway spruce	Bud burst (field)	2004	E-OBS (0.1°)	Temperature	1989-2018
			Frost damage (field)	2004	Loggers Skogsforsk	Temperature	2013-2018
			Height (field)	2007 2014	CORDEX (0.11°)	Temperature	1989-2100
IV	SWE-NPN	Norway spruce	Bud burst (field) Senescence onset (field)	1873-1951	CRU TS 3.23 (0.5°)	Temperature Precipitation Cloud fraction	1901-1951
	SWE-NPN	Norway spruce	Bud burst (field) Senescence onset (field) Senescence completion (field)	2008-2020	E-OBS (0.25°)	Temperature Precipitation Global radiation	1950-2020
					CORDEX (0.25°)	Temperature Precipitation Radiation	1989-2100

To study the differences in the spring and autumn phenology among populations and provenances of boreal and temperate trees, attributed to adaptation to local environmental conditions, phenological data from the field trials where trees of a different geographical origin are grown under the same conditions can be used (Hänninen, 2016; Luquez et al., 2008). In Paper II, we used phenological data from Sävar (63.9 °N) common garden experiment, with observations on the timing of bud set in aspen trees from the Swedish Aspen Collection. The collection consists of 116 natural aspen genotypes originating from 12 different populations along the latitudinal (55.9-66°N) and altitudinal (5-500 m above sea level) clines in Sweden (Luquez et al., 2008). In Paper III, we applied data from three Norway spruce provenance trials in southern Sweden, with plant material collected from 18 different Swedish and East-European provenances, spanning latitudinal (49.6-60.5°N) and longitudinal (12.3-30.3°E) gradients. The dataset included observations on bud burst/shoot development and frost damage during third growth season, and height growth of the seedling after six and 13 growth seasons.

To determine possible trends in the timing of phenological events in relation to the corresponding trends in environmental variables, such as temperature, phenological data collected over several decades within phenological networks can be utilized (Hanes et al., 2013). Phenological records are usually compiled by professional and volunteer observers, using standard written instructions. In Paper IV, we used a long-term historical phenological dataset (1873-1951) from the Swedish National Phenology Network (SWE-NPN), with observations on bud burst and onset of leaf senescence from aspen trees. We also obtained present-day data on aspen phenology (2008-2020) from SWE-NPN, including information on the timing of bud burst, and onset and completion of leaf senescence. However, shorter phenological time series, collected over one or two decades, may not be sufficient to display statistically significant trends in response to temperature due to large interannual variation in both phenology and temperature. The data is however of value for parameterisation of phenological models (Hanes et al., 2013).

To support the development of a phenological model, data on trees grown under controlled conditions in a greenhouse or growth chamber can be incorporated in addition to field observations, as they enable a direct assessment of the effects of temperature and photoperiod on tree phenology (Hänninen, 2016). In Paper II, data on the photoperiod inducing bud set and the time until bud set from greenhouse and growth chamber experiments were used to model the timing of bud set in aspen.

Climate data

Different climate datasets (Table 1) were used in Papers II-III to enable the comparison with phenological data.

To relate the phenological observations from the field trials to observed environmental conditions, the climate data from the local meteorological station are commonly used. If the local data are of insufficient quality (e.g. due to gaps in the dataset) or not available, it might be possible to use data from the nearest available meteorological station or to use gridded observed climate data. In Paper II, we used temperature and precipitation data from Umeå Flygplats station run by the Swedish Meteorological and Hydrological Institute (SMHI). The SMHI temperature data were compared with the local temperature data and transformed with the linear scaling method to represent the local field site condition. In Paper III, we applied gridded observed temperature data from the European gridded observational dataset (E-OBS) (Cornes et al., 2018). The E-OBS data were compared with local temperature data from filed sites with temperature loggers using the Cumulative Density Functions matching approach, to examine potential systematic differences between the datasets.

Gridded observed data were also used in Paper IV, to assess spatial and temporal phenological trends. Two datasets were selected, the CRU TS 3.23 (Mitchell and Jones, 2005) and E-OBS, to enable the analysis during the historical and current time periods, respectively. Both datasets were also used as an input to the ecosystem model to generate historical and present-day simulations of leaf cover development and gross primary production.

To assess the climate change impact on tree phenology, the reference and future model simulations can be generated using the gridded climate model data. The global and regional components of the climate model data contribute to uncertainties. The global model uncertainty is associated with the differences in the representation of the large-scale dynamics, while the variation in methods representing the small-scale dynamics and physics leads to the regional model uncertainty (Déqué et al., 2007; Déqué et al., 2012). To address these types of uncertainties, an ensemble approach can be applied, that is combining data from multiple climate models (Araújo and New, 2007).

In Paper III and IV, the gridded climate model data were obtained from the Coordinated Regional Climate Downscaling Experiment (CORDEX) (Giorgi et al., 2009). In Paper III we used an ensemble of temperature data, that consisted of the data from one regional climate with boundary conditions defined by three different global climate models. In Paper IV, we included data from one regional climate model driven by one global climate model. In both papers, we focused on the climate scenario projecting the highest temperature increase of 4.3°C ± 0.7°C by 2100 relative to pre-industrial temperatures, i.e. the Representative Concentration Pathways 8.5 W/m2 (RCP8.5). Since different RCPs are characterised by similar temperature increase by the middle of the century, generating transient simulations under RCP8.5 enables to consider all other RCPs.

Data analysis

Papers II-IV of the thesis use statistical methods and modelling approaches to analyse the phenological responses of trees to different environmental cues under current and future climate conditions.

The inter-annual variations within the phenological observational material were described with elementary statistics (mean, standard deviation), while the spatial variations along the climatic gradients (latitudinal and longitudinal) were assessed with the linear regression models. Depending on the length of the phenological dataset, different methods were used to find a link between the temporal variations in the timing of phenological events and preceding environmental conditions. In Paper II, the growing season temperature and precipitation anomalies, calculated as a difference between the normal temperature/ precipitation and the temperature/ precipitation in a given year, were used to explain the variation in bud set between three years. In Paper IV, phenological responses to temperature were assessed using linear regression of phenological onset dates on the temperature of the preceding months for each phenological time series longer than four years.

The relevant period for the phenological event (sufficient to provide an environmental signal) is several weeks or months before the phenological event, and it may vary among species and locations (Fu et al., 2015). The mean temperature of the three months, including the two preceding months and the month of the phenological event, is commonly used (Paper IV) (Jochner et al., 2016). However, since the amplitude of daily temperature fluctuations often exceeds the differences in the monthly average temperature over a couple of adjacent months, it has been suggested to use moving averages of temperature (averaging past temperatures for a specific period of time), to account for short-term fluctuations and capture the seasonal cue of temperature. Four-six weeks moving averages are generally considered as the most appropriate (Paper II) (Kudoh, 2016).

Frost damage in spring occurs if the following criteria are fulfilled: a sufficient number of days with warm temperatures to initiate early bud development, a sufficient number of frost-free days for the development to proceed to a vulnerable phase (bud burst), and occurrence of subsequent frost days. The risk of spring frost damage is evaluated based on the frequency with which these conditions are met (Augspurger, 2013). In Paper III, the risk of spring frost damage for different Norway spruce provenances was assessed by the number of frost events (defined as days with minimum temperature below −2°C and 0°C) occurring after bud burst. To identify the frost prone site, the total number of frost events occurring between January1-June 29 was estimated for each field site with provenance trials.

Phenological modelling

Modelling the timing of bud set and bud burst

In Paper II, a concept of temperature-dependent delay of growth cessation was addressed, as such an effect was revealed from the data analysis and has been also demonstrated by several experimental studies (Resman et al., 2010; Rohde et al., 2011a). Two models incorporating daylength and temperature in simulating the timing of bud were developed: Model 1 assumed a peaked temperature response (i.e. lower as well as higher than the threshold temperature for growth cessation delay the onset of growth cessation to shorter critical daylength), and Model 2 used a linear temperature response function (i.e. the critical daylength for growth cessation decreases with increasing temperature). Model based on the critical daylength only (Null model) was included for comparison. The stages of autumnal bud development were defined based on a literature review (Paper I).

In Papers III and IV, two different descriptions, sequential and parallel, of the relationship between chilling and forcing temperatures were applied to model the timing of bud burst, based on the background knowledge of species responses. The amount of chilling was expressed as chilling days (days with mean temperature below 5°C) or chilling units (chilling temperatures from – 3.4°C to 10.4°C), and the amount of forcing was calculated as an accumulation of daily mean temperature above 5°C (Cannell and Smith, 1983; Hannerz, 1999; Hänninen, 1990).

In Paper III we used the temperature sum model based on the linear temperature response with January 1 as a starting day for temperature sums accumulation, for predicting the date of bud burst for Norway spruce. The chilling requirement for Norway spruce has been suggested to be fulfilled in late autumn or early winter under current climate conditions in southern Sweden (Hannerz, 1999; Hannerz et al., 2003). This was validated by separately calculating chilling units and chilling days between September 1-December 31. In this approach, the temperature sum model can be considered as a simplification of the sequential model. In Paper IV, the forcing requirement for bud burst for aspen trees was modelled as an inverse exponential function of the length of the chilling period (chilling days), thus representing parallel approach.

Model calibration and evaluation

In the phenological modelling approach the optimisation of the model parameters, calibration, is performed by fitting the model to observed phenological and climate data (Hänninen, 2016). The parameters values that minimized the root mean square error (RMSE) between observed and modelled phenology are then selected. Models should be evaluated against independent data, i.e. data that was not used to calibrate the model (Evans et al., 2014). All models in the thesis were evaluated using external data. The standard evaluation metrics were used: RMSE, Pearson correlation coefficient (r^2) and model bias between the observed and modelled timing of phenological events. In Paper II, to account for the different number of model parameters, models were also assessed based on Akaike information criterion corrected for finite sample sizes.

Climate change impact assessment

To generate the reference simulations and future projections, the model is combined with climate model data. Analysis of the model output at different time periods enables to capture the climate change signal. In Paper III, the temperature sum model, parameterized with the estimated provenance specific temperature sum requirements for bud burst, was driven by the ensemble of gridded climate model data to simulate the timing of bud burst and spring frost events. In Paper IV, the ecosystem model with calibrated phenological parameters was used together with the climate model data to simulate the timing of bud burst, annual leaf area index and annual gross primary production. Both papers included simulations for the far future (till 2100), and the outputs were analysed over the 30-years period by comparing future and reference periods.

Results and discussion

Regulation of growth cessation and bud set

Molecular basis

The role of the seasonal reduction in photoperiod as a primary cue in the regulation of growth cessation and bud set phenology in various tree species has been demonstrated by many previous studies (Cooke et al., 2012; Ding and Nilsson, 2016; Petterle, 2011), and it has been intensively studied at the molecular level in *Populus* trees (Azeez et al., 2014; Böhlenius et al., 2006; Karlberg et al., 2010; Randall et al., 2015; Tylewicz et al., 2015). The current knowledge on the molecular regulation of growth by photoperiod was reviewed in Paper I. The circadian clock and phytochrome photoreceptors were described as early components mediating photoperiodic control of growth (Howe et al., 1996; Ibáñez et al., 2010; Olsen et al., 1997; Takata et al., 2009). Key components of the photoperiodic signalling pathway of growth control in trees were summarised in the simple model of short days induced growth cessation (Fig.2).

A number of studies have shown the effect of temperature on growth cessation and bud set, although the results are equivocal, as both accelerated and delayed bud set by warm temperatures, as well as low temperature induced bud set have been reported (Junttila et al., 2003; Kalcsits et al., 2009; Mølmann et al., 2005; Rohde et al., 2011b; Sivadasan et al., 2017). The potential interactions between photoperiodic- and temperature-mediated signalling pathways in the control of growth cessation remains to be explored at a molecular level.

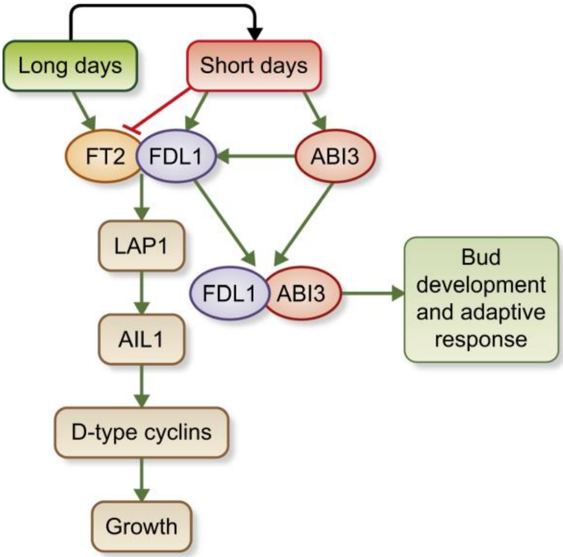

Figure 2.
Transcriptional network underlying the photoperiodic control of growth in poplar. A shift to short days represses *FT2* expression, resulting in the downregulation of *LAP1* (LIKE-AP1) and the LAP1 target AIL1 (AINTEGUMENTA-LIKE1). Downregulation of *AIL1* leads to the suppression of cell cycle-related genes and growth cessation. The expression of FD-LIKE1 (FDL1) and ABA INSENSITIVE 3 (ABI3) is induced by short days, and they form a transcriptional complex involved in the regulation of bud maturation and cold acclimation-related programs. Reproduced from Paper I.

Modelling approach

The role of temperature in modulating photoperiod-induced growth cessation and bud set was studied in Paper II. The timing of bud set observed in the field differed from the expected dates of bud set, estimated based on the photoperiod at bud set in the growth chamber experiment. The interannual variation in the observed bud set was linked to the preceding temperature conditions, i.e. earlier bud set was associated with lower temperature, while a delayed bud set coincided with a warm spell in the preceding month. Together, these results indicated a potential temperature effect on growth cessation and bud set, which was further considered in the models of autumnal bud development. Evaluation of the developed models revealed that integrating both photoperiod and temperature improves the predictions of bud set date, but only in non-stressful conditions. The temperature response was shown to occur within a short period of time relative to the critical daylength for growth cessation, and additional regulatory mechanisms may be involved under stressful conditions. The modelling framework presented in Paper II provides a basis for future modelling studies on autumn phenology.

Variation in phenology among populations and provenances

Analysis of phenological data

The timing of phenological events, such as bud set, leaf senescence and bud burst, varied among populations and provenances in Papers II-IV (Table 2), indicating an adaptation to the local climate conditions. Both environmental and genetic factors have been shown to contribute to spatial variation in phenology, and loci associated with the local adaptation are being identified by the studies that involve large-scale sequencing and phenotyping of the trees genotypes along latitudinal clines (Evans et al., 2014b; Ingvarsson et al., 2006; Pelgas et al., 2011).

Table 2.
General patterns of variation in phenological response to environmental cues among populations and provenances of boreal and temperate trees, expressed by the difference in timing of phenological events and corresponding values of the parameters.

Population/ provenance	**Bud set**			**Bud burst**			**Senescence**	**Growing season**
	Critical daylength	T_{opt} for gross cessation	Timing	Chilling requirement	Forcing requirement	Timing	Timing	Length (days)
Northern Sweden	Long	Low	Early	Low	Low	Early	Early	Short
Southern Sweden	Short	High	Late	Intermediate	Intermediate	Late	Late	Long
East Europe	-	-	-	High	High	-	-	-

In Paper II, the timing of bud set in different populations of European aspen from the Swedish Aspen Collection followed a latitudinal gradient, with the populations from northern latitudes having earlier bud set compared to the populations from southern latitudes, reflecting the adaptation to the daylength conditions. The molecular basis of the latitudinal cline in the timing of bud set has been explained by the findings of Böhlenius et al. (2006). Their data showed that the diurnal expression of the gene *CONSTANS (CO)* in aspen trees collected from different latitudes varied according to latitudinal cline and coincided well with critical day length at these latitudes, which defines the timing of growth cessation in these genotypes. Moreover, the downregulation of *CO* resulted in earlier growth cessation in hybrid aspen.

In Paper III, the Norway spruce provenance specific temperature sum requirements for bud burst were significantly different and correlated with the latitude and longitude of the place of origin, thus indicating the differentiation in the timing of bud burst among the provenances. Spruce trees of East-European origin had higher temperature sum requirement for bud burst than trees originating from Sweden, as the onset of warm temperatures in spring occurs later and progresses faster in the north (Jönsson and Bärring, 2011).

In Paper IV, the timing of bud burst and onset of senescence in aspen trees from the Swedish National Phenology Network displayed significant differences between trees from southern and northern groups of sites. These results were consistent with the strong genetic differentiation between the southern and northern populations of aspen trees from the Swedish Aspen Collection, which has been identified in previous studies (Ingvarsson and Bernhardsson, 2020; Luquez et al., 2008).

Modelling approach

The differences in phenological response to daylength and temperature among populations and provenances were addressed in Papers II and III by using the population- and provenance specific values of the model parameters (Table 2).

In Paper II, the population specific values of the critical daylength for growth cessation for aspen trees, estimated from the linear interpolation of the values suggested by Böhlenius et al. (2006), were lower for southern populations than for the northern populations. In addition, the calibrated population specific range of temperature within which the critical daylength induced growth cessation was similar between southern and northern populations in Sävar common garden (63.9 °N). However, previous studies have shown that the optimal temperature (Topt) for sensing the critical daylength was higher for southern populations compared to northern populations, as it may be genetically determined or depend on the local climate conditions (Kalcsits et al., 2009; Rohde et al., 2011a). The disparity between the results can be explained by the effect of Sävar common garden experiment, where the critical daylength for growth cessation for southern populations occurs later in summer when the temperature starts to decrease. Evaluation of the performance of developed models at site scale indicated higher accuracy with the population specific calibration compared to the calibration at a general level. Since the calibrated model parameters were site specific, the model may not be able to capture large-scale variation, therefore the model validity at different spatial scale needs to be assessed.

In Paper III, the provenance specific temperature sum requirements for bud burst estimated from the Norway spruce provenance trials were similar between the sites, and the effect of site on the relative temperature sums was insignificant. These suggested that the temperature sum model parameterised with the average provenance specific temperature sum requirements for bud burst can be used to calculate the provenance specific risk of spring frost damage at an arbitrary site. Lower temperature sum requirements for bud burst were associated with a higher risk of frost damage, with trees being exposed to lower temperatures and more frequent frost events during the frost susceptible period compared to late bursting provenances. The importance of the local climate conditions was also apparent (Fig. 3). In this approach, frost prone site and provenances with a lower risk of being exposed to spring frost events were identified, this information can then be used to develop recommendations on the selection of suitable plant material to reduce spring frost damages.

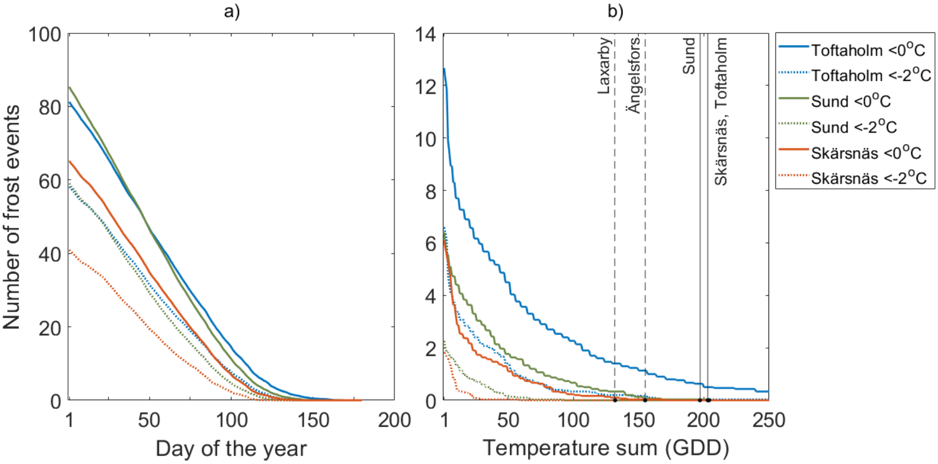

Figure 3.
The annual average number of frost events between January 1 - June 29 (DOY 180) below 0 °C and −2 °C over 30 years (1989–2018), calculated from EOBS data: a) in relation to the day of the year, b) in relation to the accumulated temperature sum, expressed as growing degree days (GDD) above +5 °C. Dashed vertical lines indicate the average temperature sum required for bud burst in two different provenances: Laxarby (with the earliest date of bud burst) and Ängelsfors (most northern origin). Solid vertical lines indicate the average temperature sum required for bud burst at the three different sites, given all individual trees. Modified from Paper III.

In Paper IV, the calibration of phenological parameters, using the accumulated temperature sums and chilling days at the observed timing of bud burst, substantially improved the performance of the ecosystem model in term of simulating spring leaf cover development compared to the original parameterisation. The multi-site calibration (i.e. based on data from all sites) captured the large-scale variation in the timing of bud burst, as the calibration by groups of southern and northern sites did not affect the model accuracy. The biases in the modelled leaf cover onset were removed, affecting the seasonal dynamics of gross primary production and annual estimates. The calibrated phenology led to a decrease in annual carbon uptake, mainly due to later leaf cover onset, indicating the potential constraints to forest productivity under future climate conditions. These results are in line with the previous studies, that have also demonstrated the importance of having accurate phenology representation for improved ecosystem model performance (Keenan et al., 2012; Renwick et al., 2019; Richardson et al., 2012).

Climate change impact on tree phenology

The potential effects of climate change on tree phenology and forest productivity were assessed in Papers III and IV. In both papers reduced chilling accumulation (expressed as chilling days) was shown in response to temperature increase. In Paper III, the model simulations indicated that the upper limit of the chilling requirement for Norway spruce will still be fulfilled in the near future (2021-2050) and in 60-70% of years during the far future (2071-2100). Therefore, the bud burst projections based on the temperature sum requirement for bud burst were considered as reliable. The timing of bud burst for Norway spruce provenances will occur earlier in the near- and far future and will be associated with increased risk of spring frost damage due to increased frequency and severity of frost events after bud burst (Fig. 4). As Norway spruce stand rotation times are 60-90 years, the knowledge on the provenance specific frost risk under climate change is important to support forest management decisions on having suitable plant material for regeneration in the coming decades.

In Paper IV, the reduction in accumulated chilling days for aspen trees from 1901-1951 to 2008-2020 was underlying the decline in temperature sensitivity of bud burst between the periods. The simulations of the calibrated ecosystem model projected about two weeks earlier bud burst and enhanced mean annual gross primary production across Sweden during 2071-2100 compared to the current climate conditions (Fig. 5). However, it remains uncertain whether the temperature sensitivity of bud burst observed under current climate conditions continues to hold in the future, which in turn contributes to the uncertainty in future projections of forest productivity. This highlights the importance of understanding the mechanisms underlying the environmental regulation of dormancy release and bud burst, and their implementation in the ecosystem models.

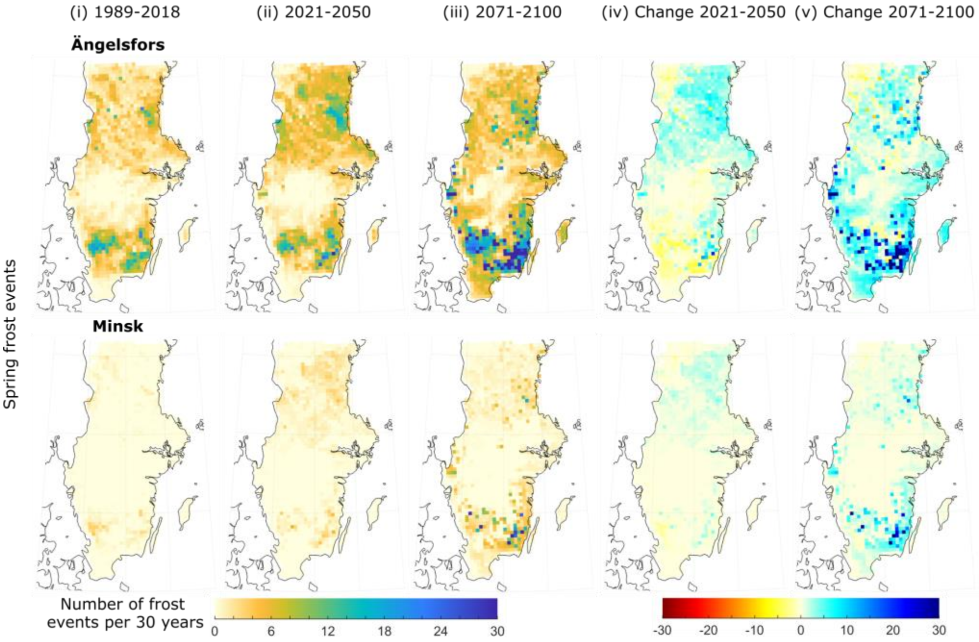

Figure 4.
The cumulative number of frost events below −2 °C between bud burst and June 29 over 30 years in southern Sweden for the earliest and latest Norway spruce provenances assessed in the study for the periods (i) 1989–2018, (ii) 2021–2050, (iii) 2071–2100, and the diffrence between (iv) 2021–2050 and 1989–2018, (v) 2071–2100 and 1989–2018. The results are based on the climate model temperature data representing RCP8.5. Modified from Paper III.

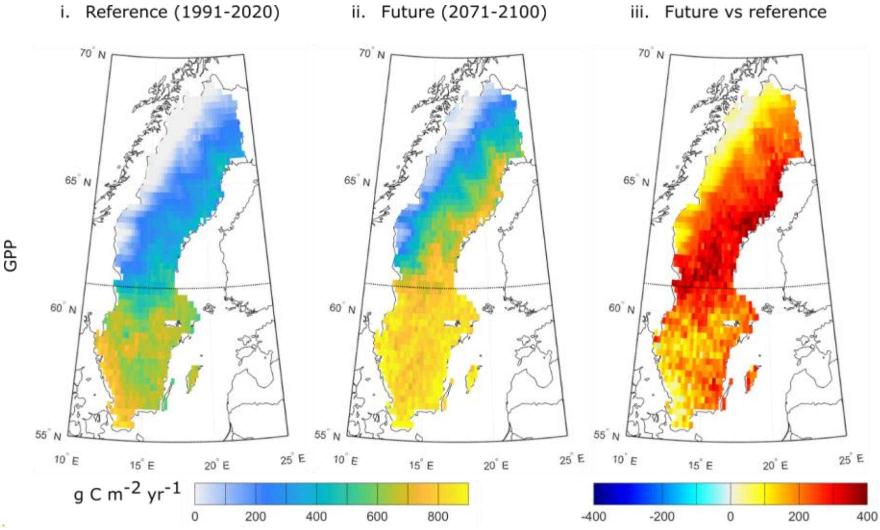

Figure 5.
The average annual gross primary production (GPP, g C m^{-2} yr^{-1}) in Sweden for (i) the reference (1991-2020) and (ii) future (2071-2100) periods, and (iii) the difference between future and reference periods. Results are based on the climate model temperature data representing RCP8.5. The horizontal line indicates latitude 61°N, a border between Southern and Northern Sweden. Modified from Paper IV.

Conclusions and outlook

This thesis demonstrated how the different research methods can be used to improve our understanding of environmental regulation of the timing of key developmental stages of the annual growth cycle of trees in temperate and boreal forests. The literature review provided a novel synthesis of current knowledge of the molecular-level regulation of the annual growth cycle, by presenting models of molecular components underlying the photoperiodic control of growth, bud dormancy establishment, and control of bud dormancy release and activation of bud burst. The knowledge gaps identified in the review, such as in the understanding of the interactive effect of temperature on the regulation of photoperiod-induced growth cessation and bud set, were addressed by means of modelling.

The thesis showed that the knowledge on the regulation of tree phenology by environmental factors can be applied to generate climate change impact assessments, including potential changes in the timing of phenological events and implications for forest productivity. The finding from the modelling studies highlighted the importance of considering the population- and provenance specific differences in response to environmental signal in the model calibration. The species-specific differences in response to climate change were indicated. The need for improved phenology representation in the ecosystem models for more accurate projections of gross primary production was revealed.

Further progress towards a better understanding of regulation of tree phenology can be achieved through integrating molecular and modelling approaches, by incorporating recent advances in elucidating molecular pathways of environmental regulation of stages of the annual growth cycle into phenological models.

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