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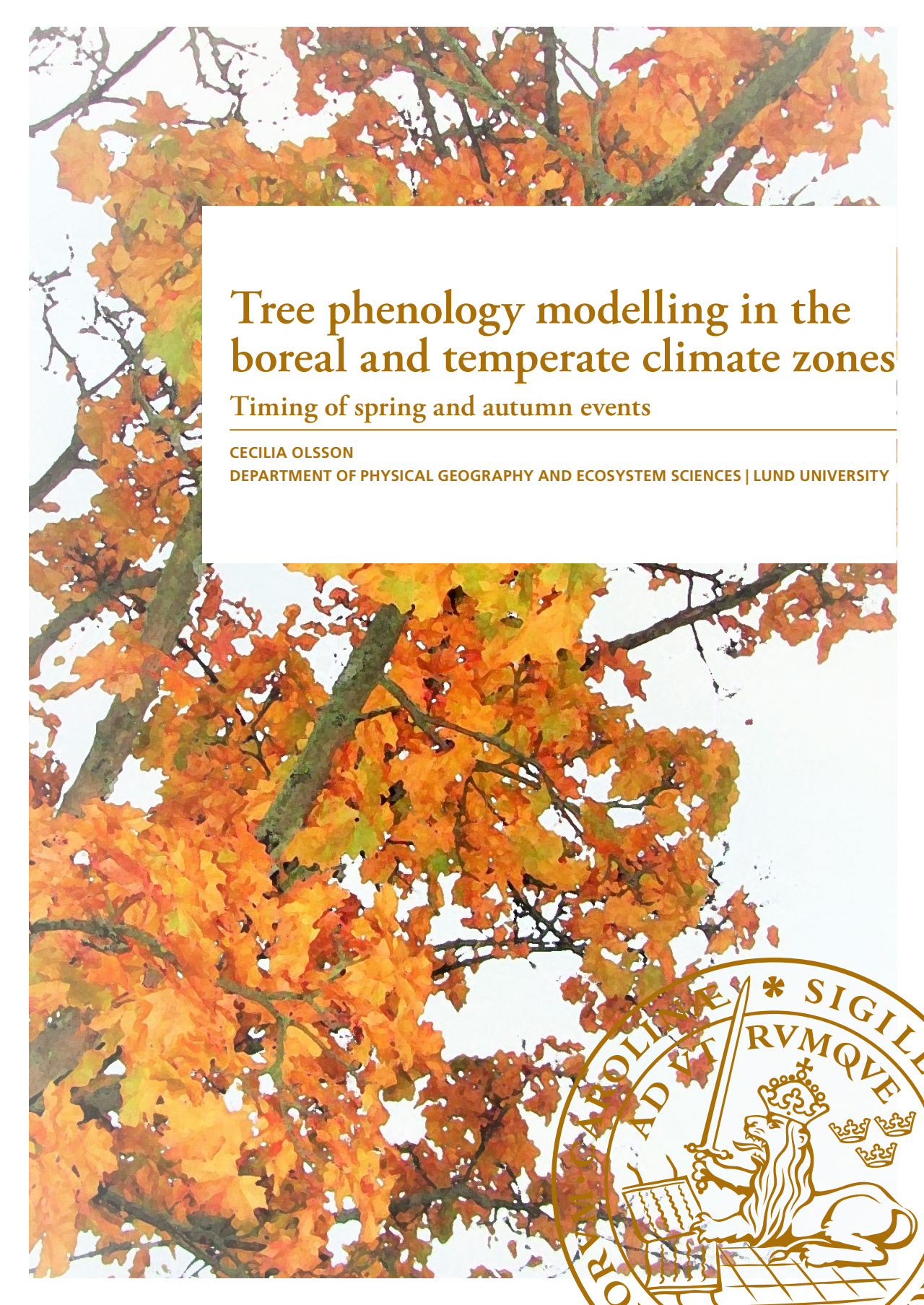
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Tree phenology modelling in the boreal and temperate climate zones

Timing of spring and autumn events

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DEPARTMENT OF PHYSICAL GEOGRAPHY AND ECOSYSTEM SCIENCES | LUND UNIVERSITY



Tree phenology modelling in the boreal and temperate climate zones

Timing of spring and autumn events

Cecilia Olsson



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DOCTORAL DISSERTATION

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To be defended at Pangea auditorium, Friday 14 November at 10:00.

Faculty opponent

Associate Professor Andrew Richardson,

OEB, Harvard University, Boston, USA

Organization LUND UNIVERSITY Department of Physical Geography and Ecosystem Science, Sölvegatan 12, SE-223 62 Lund, Sweden Author(s) Cecilia Olsson	Document name DOCTORAL DISSERTATION Date of issue: 2014-10-06 Sponsoring organization
Title and subtitle: Tree phenology modelling in the boreal and temperate climate zones : Timing of spring and autumn events	
<p>Abstract</p> <p>Plant phenology in the boreal and temperate climate zones is synchronised with seasonal changes in temperature and photoperiod. For deciduous trees, timing of budburst and leaf colouring define the growing season length and express adaptations to trade-offs in growth and risks. An extended growing season due to climate warming will likely increase forest productivity, however these potential benefits may be outweighed by an increase in risks such as frost damage.</p> <p>In order to estimate the impact of climate change on forest phenology, the reliability of phenology models needs to be assessed. In this thesis, the ability of phenology models to capture inter-annual and spatial variation in budburst and leaf colouring were evaluated for five tree species that are important in Swedish forest management; birch, beech, oak, Norway spruce and Scots pine. Model simulations were assessed in relation to model structure, the models representation of tree physiology processes and the calibration -, temperature - and phenology data used. The novelty of the thesis is that simulations were carried out across large regions using extensive phenological datasets which consist of observations of more than 1000 trees, with up to 60 observation-years per tree.</p> <p>The results indicate that the model structure influence the models sensitivity to calibration data and to temperature conditions. Spatial differences in trees response to environmental cues is not well represented in the models. The models do not consider differences in provenance-specific requirements and therefore was the accuracy of the simulations influenced by the models being tuned to the average phenological response of the calibration data. Overall, the budburst models overestimated the temperature effect. In colder regions where budburst usually occurs later, budburst was simulated to occur too late, and in warmer regions where budburst occurs earlier, budburst was simulated to occur too early. The more accurate budburst models were in general structurally simple. They considered the effect of warm spring temperatures, thereby assuming full dormancy release without considering winter conditions. Leaf colouring was better estimated by average day of leaf colouring than by the model simulations.</p> <p>In conclusion, the results indicate that the models do not capture the phenology across large regions well enough to be considered reliable for climate change assessments, emphasising the lack of mechanistic understanding of phenological processes.</p>	
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Timing of spring and autumn events

Cecilia Olsson



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A doctoral thesis at the university in Sweden is produced either as a monograph or as a collection of papers. In the latter case the introductory part constitutes the formal thesis, which summarizes the accompanying papers already published or manuscripts at various stages (in press, submitted, or in preparation).

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- III. CO contributed to the study design, performed all simulations and analysis, contributed to the interpretation of the results and led the writing.
- IV. CO led the design of the study, performed all simulations and analysis, contributed to the interpretation of the results and led the writing.

Abstract

Plant phenology in the boreal and temperate climate zones is synchronised with seasonal changes in temperature and photoperiod. For deciduous trees, timing of budburst and leaf colouring define the growing season length and express adaptations to trade-offs in growth and risks. An extended growing season due to climate warming will likely increase forest productivity, however these potential benefits may be outweighed by an increase in risks such as frost damage.

In order to estimate the impact of climate change on forest phenology, the reliability of phenology models needs to be assessed. In this thesis, the ability of phenology models to capture inter-annual and spatial variation in budburst and leaf colouring were evaluated for five tree species that are important in Swedish forest management; birch, beech, oak, Norway spruce and Scots pine. Model simulations were assessed in relation to model structure, the models representation of tree physiology processes and the calibration -, temperature - and phenology data used. The novelty of the thesis is that simulations were carried out across large regions using extensive phenological datasets which consist of observations of more than 1000 trees, with up to 60 observation-years per tree.

The results indicate that the model structure influence the models sensitivity to calibration data and to temperature conditions. Spatial differences in trees response to environmental cues is not well represented in the models. The models do not consider differences in provenance-specific requirements and therefore was the accuracy of the simulations influenced by the models being tuned to the average phenological response of the calibration data. Overall, the budburst models overestimated the temperature effect. In colder regions where budburst usually occurs later, budburst was simulated to occur too late, and in warmer regions where budburst occurs earlier, budburst was simulated to occur too early. The more accurate budburst models were in general structurally simple. They considered the effect of warm spring temperatures, thereby assuming full dormancy release without considering winter conditions. Leaf colouring was better estimated by average day of leaf colouring than by the model simulations.

In conclusion, the results indicate that the models do not capture the phenology across large regions well enough to be considered reliable for climate change assessments, emphasising the lack of mechanistic understanding of phenological processes.

Sammanfattning

I den boreala och tempererade klimatzonen är växternas fenologi synkroniserad med årstidsväxlingar i temperatur och dagslängd. För lövträd påverkar tidpunkten för knoppsprickning och lövfärgning både tillväxt och risktagande. En förlängd växtsäsong till följd av ett varmare klimat innebär sannolikt högre produktivitet inom skogsbruket, men kan också leda till ökad risk för exempelvis frostsador.

För att uppskatta klimatförändringarnas effekt på skogens fenologi behövs tillförlitliga fenologimodeller. I den här avhandlingen utvärderades hur väl fenologimodeller fångar mellanårs och rumslig variation i tidpunkt för knoppsprickning och lövfärgning för fem trädarter viktiga inom svensk skogsbruk; björk, bok, ek, gran och tall. Modellsimuleringarna analyserades i relation till modellkonstruktion, modellernas representation av trädens fysiologiska processer och till den kalibrerings-, temperatur- och fenologidata som användes. För att kunna göra en bra utvärdering användes observationer från fler än 1000 träd runt om i Europa, med upp till 60 års observationer per träd.

Resultaten indikerar att modellernas konstruktion påverkar modellerna känslighet för kalibreringsdata och temperaturförhållanden. Modellerna lyckades inte fånga rumsliga skillnader i trädens respons till temperatur och dagslängd. Eftersom modellerna inte tar hänsyn till att träd med olika härkomst kan ha olika ljus- och temperaturbehov, påverkades precisionen i simuleringarna av modellkalibreringen genom att modellerna anpassats till den genomsnittliga fenologiska responsen i kalibreringsdata. Överlag överskattade knoppsprickningsmodellerna temperatur-effekten. I kallare regioner där knoppsprickning sker relativt sent simulerades knoppsprickning för sent och i varmare regioner där knoppsprickning sker tidigare simulerades knoppsprickning för tidigt. De bättre knoppsprickningsmodellerna var relativt enkla i sin konstruktion och inkluderade effekten av varma vårdagar medan vintervilan antogs var helt bruten genom att inte inkludera vinterförhållanden. Tidpunkt för lövfärgning uppskattades bättre av medeldag än med modellsimuleringar.

Sammanfattningsvis indikerar resultaten att modellerna inte simulerar fenologi tillräckligt bra för att kunna anses vara tillförlitliga i klimatförändringsstudier, vilket betonar bristen på mekanistisk förståelse av fenologiska processer.

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Introduction

Phenology is the study of timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species. (Lieth, 1974)

For plants to survive in boreal and temperate regions, it is important that the annual growth cycle is synchronised with the seasonal changes in temperature and photoperiod. This thesis focuses on budburst and leaf colouring timings, adaptive traits to trade-offs in growth and risks, which approximates the onset and end of the growing season. For example, an early onset can maximise growth and give a competitive advantage over trees with a later onset, but an earlier onset increase the risk of damage by frost and insects (Keskitalo *et al.*, 2005). Early growth cessation and leaf senescence shorten the growing season, but allow the tree to fully remobilise nutrients that are stored for use in the following spring. Late senescence prolongs the growing season but instead increases the risk for frost damage and potential leaf fall before nutrient remobilisation (Larcher, 2003).

Phenological research, past and present

Early on, people recognised the influence of weather on plant development and put the understanding into practice, e.g. in agriculture for determining sowing time. The longest existing and still ongoing phenological record is from Japan, where flowering of cherry trees have been observed and recorded for more than 1300 years. Carl von Linné is often considered the father of modern phenological studies for defining methods for compiling observations of climate and phenology. In the middle of the 18th century, Linné established the first phenological network, and since the middle of the 19th century, many networks have been established and guidelines for phenological observations have refined (Koch *et al.*, 2009). Phenology is today widely studied and appreciated by the general public, with many volunteers recording observations that create data sets with great spatial coverage and long time-series (Sparks & Menzel, 2002).

The concept of phenology varies among researchers and develops with technical and methodological advancements. The spatial scale in phenological research varies from individuals to ecosystems, with the relation between phenology and

environmental cues varying among scales (Pau *et al.*, 2011). The physiological cycle of individual trees is commonly observed by manual ground observations. At ecosystem level, seasonal changes in vegetation activity are usually studied using remotely sensed greenness that depends on the absorption and reflection of photosynthetically active radiation (Stöckli & Vidale, 2004) (Fig. 1). The spatial coverage of remotely sensed phenology is an advantage, but the temporal resolution is relatively low compared to manual observations, often every 8th or 16th day. In addition, the reflectance is influenced by e.g. species composition and land cover type, which can only be determined by field observations (Isaacson *et al.*, 2012). Other monitoring methods include installed cameras, which provide daily reflectance of known vegetation, and eddy covariance measurements, which describes biochemical fluxes from soil and vegetation (Cleland *et al.*, 2007).

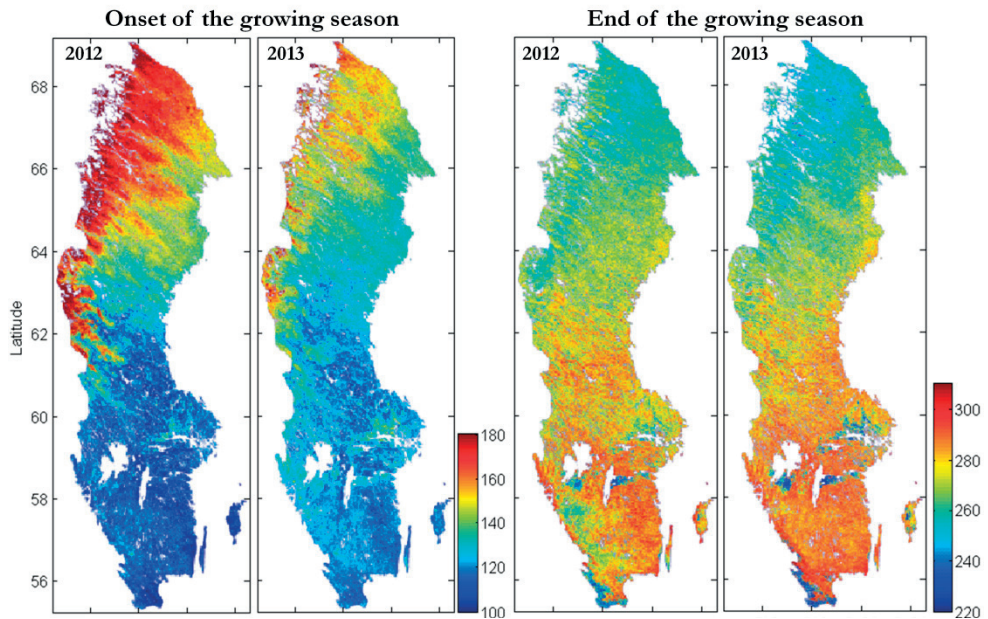


Figure 1. Satellite derived approximate day of year onset and end of the growing seasons in Sweden, year 2012 and 2013, using MODIS nadir BRDF-adjusted reflectance and plant phenology index (PPI) (Jin & Eklundh, 2014) with a threshold of 0.15 for all vegetation. Pixels classified as water and build-up area are excluded, and those covering cropland harvested at the end of the growing season are shown in blue. Images by Hongxiao Jin (pers. comm.).

Phenological trends and patterns

In general, phenological events occur earlier in the order; birch, beech and oak, with spring phenology of Norway spruce and Scots pine in general later than oak.

As the phenology in the boreal and temperate climate zone is strongly influenced by seasonality, spatial patterns follow that of primarily temperature, with more pronounced patterns for spring than for autumn events (Estrella & Menzel, 2006). In general, the growing season starts later from south to north, and later in more continental regions (Fig. 1). Relative to low elevation, trees at higher elevations flush later and start leaf senesce earlier and therefore is the growing season often shorter (Vitasse *et al.*, 2009). Early plant spring events are in general more spatial variable than later occurring spring events, and early autumn events are in general less variable than later occurring autumn events. With climate warming, the spatial variation might increase since the overall trend is advancing spring events and delayed autumn events (Menzel *et al.*, 2006).

The strong influence of temperature makes changes in phenology a good bio-indicator of climate change. The growing season of many plants in the Northern hemisphere has since the 1950's extended, mainly due to advancing onset, but the rate of change vary among species, regions and time-periods (e.g. Ahas *et al.*, 2002, Linderholm, 2006, Menzel *et al.*, 2008, Menzel & Fabian, 1999, Menzel & Fabian, 2001, Parmesan, 2007, Parmesan & Yohe, 2003) (Fig. 2). Changes are in general more pronounced further north (White *et al.*, 1999). Genetically identical clones planted in phenological gardens in Europe, flushed on average 0.2 days/year earlier and leaf senesced on average 0.16 days/year later, and the overall growing season extended by 10.8 days from 1959 to 1993 (Menzel & Fabian, 1999). However, not all trees follow the same trends, and during the same time-period some trees flushed later and leaf senesced earlier.

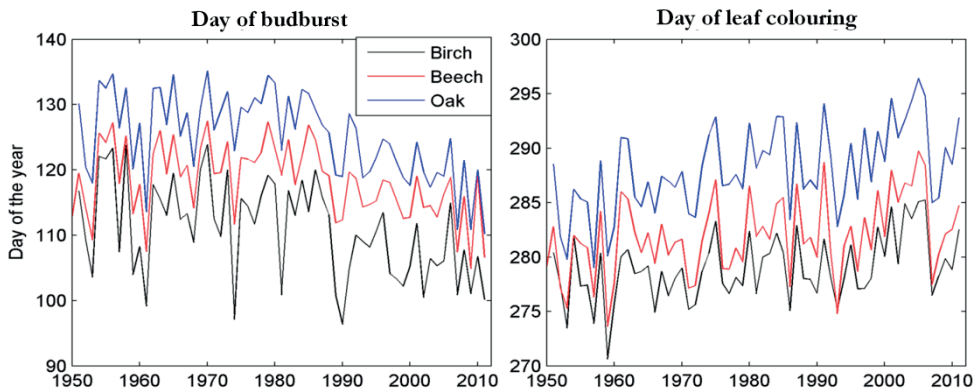


Figure 2. Average day of budburst and leaf colouring of more than 1,000 trees in Austria, Germany and the United Kingdom (sites used in Paper IV). Between 1950 and 2012, average day of budburst advanced 3.7-5.5 days/decade and day of leaf colouring was delayed by 3.7-5.2 days/decade. Phenological events occur in general earlier in the order birch, beech and oak, with spring phenology of Norway spruce and Scots pine in general later than oak.

The response to increased temperatures differs among functional groups. The advancing trend in growing season onset is more pronounced in early flushing

species like birch, compared to later flushing species like beech and oak (Fu *et al.*, 2012). Late flushing species are believed to be under more restraining controls, e.g. responding to temperature when days are longer, which makes them less influenced by climate warming (Fu *et al.*, 2012, Heide, 1993a, Heide, 1993b, Körner & Basler, 2010). For flowering time in the United Kingdom, perennial, wind-pollinated and plants close to their distributional edge responded less to changes in temperature than annual, insect-pollinated and plants close to centre of their range, respectively (Fitter & Fitter, 2002).

Climate change implications on ecosystems and forestry

Ecosystem composition and dynamics are likely to change with climate warming; species distribution is expected to shift to higher latitudes and elevations, and since species respond to warming differently there may be species mismatches, such as between pollinators and fruiting trees (Morecroft & Paterson, 2006, Peñuelas *et al.*, 2002). In general, due to long life- and reproductive cycles, tree species are less genetically adaptive than short-lived species (Kramer *et al.*, 2000), and little is known about the plasticity in the response to environmental cues.

An extended growing season will likely increase forest productivity and returns (Richardson *et al.*, 2010). However, potential benefits are followed by an increase in risks such as frost damage that can kill seedlings and increase energy and water demands to repair the damage, which subsequently will influence the productivity. Despite an overall warming, extremes in frost will occur and increase the risk and severity of frost damage since frost hardiness is negatively related to growth activity (Jönsson & Barring, 2011, Westin *et al.*, 2000). Reduced soil frost makes trees more susceptible to wind-throw, and damage is often followed by pest infestations that may become more common in the future (Jönsson *et al.*, 2012). Changes in phenology will influence the water balance of the forest (Richardson *et al.*, 2010) and the biochemical feedback to the atmosphere, such as release of carbon dioxide which may contribute further to climate warming (Keenan *et al.*, 2014, Richardson *et al.*, 2013).

More accurate estimations of the growing season timing improves simulations of species distributions, plant-atmosphere interactions and forest productivity (e.g. Chuine & Beaubien, 2001, Ibáñez *et al.*, 2010, Jeong *et al.*, 2012, Migliavacca *et al.*, 2012, Morin *et al.*, 2007, Richardson *et al.*, 2012). It will also improve risk assessments of insect outbreaks, storm and frost damage in forestry, and estimates on the effect of forest management strategies (Jönsson *et al.*, 2013).

The annual growth cycle and leaf development

To sustain longer periods with unfavourable growth conditions, trees in colder regions undergo a series of biochemical adjustments before entering winter dormancy to avoid frost damage to sensitive tissues (Vegis, 1964). Processes of e.g. growth cessation and leaf senescence occur simultaneously or in sequence, with only a few visible signs, such as bud set and changes in leaf colour. Most biological processes are influenced by temperature, with highest rate of change around a temperature optimum (Larcher, 2003).

The phenological response to cues in temperature and photoperiod is not fully understood, and the response vary e.g. among species, provenances, location, time of the year and tree age (Estrella & Menzel, 2006, Hänninen & Kramer, 2007, Ununger *et al.*, 1988, Vitasse & Basler, 2012). North European beech populations are more controlled by temperature than south European populations that are more controlled by photoperiod, as in the south, the growing season is more limited by photoperiod than by temperature (Vitasse & Basler, 2012). Growth rhythm changes with age and budburst occur in general earlier, and bud set later, in juvenile trees than in more mature trees (Ununger *et al.*, 1988, Vitasse & Basler, 2013). The influence of other environmental factors, such as water and nutrient availability, is even less understood (Hudson, 2010).

Growth cessation and bud set

The process of growth cessation starts after summer solstice, initiated by cues in photoperiod, and ends in bud set (Fig. 3). Northern populations are in general induced by longer days than more southern populations, but there are indications that warmer autumns reduce the trees sensitivity to photoperiodic cues depend on prevailing temperatures (Rohde *et al.*, 2011). Warm autumns imply more active growth, and growth cessation onset gets delayed when temperatures are closer to the temperature optimum (Partanen, 2004, Rohde *et al.*, 2011). At the same time, growth cessation is accelerated by higher temperatures before and during growth cessation (Junttila *et al.*, 2003, Kalcsits *et al.*, 2009, Rohde *et al.*, 2011), while short days in general lower the growth activity and accelerate growth cessation (Vegis, 1964). The level of growth activity also influences the development of frost hardiness that is negatively related to growth activity (Westin *et al.*, 2000).

Leaf colouring

The seasonal development is less understood for autumn than for spring. Due to more active growth, warm autumns tend to delay leaf colouring for many species

in Europe and USA (Archetti *et al.*, 2013, Cufar *et al.*, 2012, Estrella & Menzel, 2006, Menzel *et al.*, 2008). For some species, such as aspen, colder autumns often result in more intense leaf colouration, but the physiological process of colour change is not well understood (Keskitalo *et al.*, 2005). Leaf senescence is also influenced by environmental conditions during spring and summer, and depending on species and location, warm spring or early summer months can either advance (Estrella & Menzel, 2006) or delay leaf colouring (Archetti *et al.*, 2013).

Leaf senescence involves a complex interplay of hormones, many which are activated by various stressors such as drought or herbivores, which can induce shedding of the leaves (Lim *et al.*, 2007). Trees can shed their leaves prematurely in response to drought to prevent hydraulic damage (Bréda *et al.*, 2006), or as a defence against insects (Kikuzawa, 2004), which imply little or no nutrient remobilisation for the coming spring.

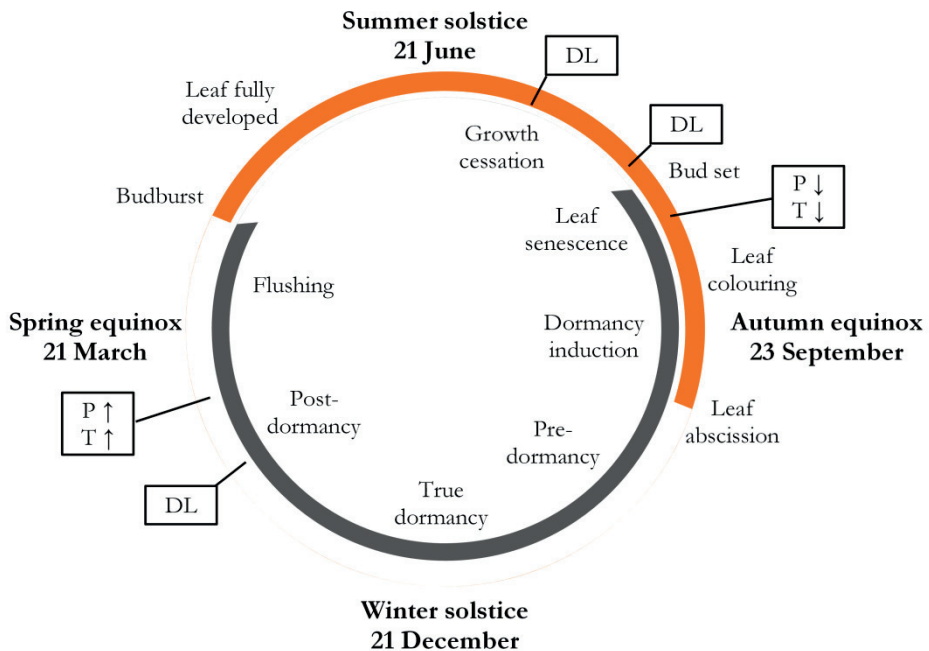


Figure 3. Conceptual figure of processes and stages of leaf development, starting with bud set, budburst, leaf colouring and ending with leaf abscission. Processes of growth cessation, leaf senescence and dormancy induction occur in sequence or parallel to each other. Indicated are potential day length requirements (DL) and if seasonal processes are mainly influenced by days becoming colder (T ↓) and shorter (P ↓), or warmer (T ↑) and longer (P ↑).

Bud dormancy

After growth cessation and bud set, buds enter a state of rest or dormancy during which they lack growth competence and are unable to develop toward budburst. In theory, dormancy release refers to changes in a dormant bud that leads to full growth competence, after which buds undergo morphological changes that ends in budburst. However, phases of dormancy are not easily observed as they do not occur in sequence but overlap and interact with each other (Vegis, 1964). One example of how winter dormancy is perceived, 1) pre-dormancy; the bud can develop but within a range of environmental conditions that become more narrow with time, 2) true dormancy; the bud is in deepest rest and irrespective of conditions cannot resume growth, and 3) post-dormancy; continues till maximum growth activity is attained and during which the bud can remain dormant, imposed by unfavourable conditions (Vegis, 1964) (Fig. 3). Other classifications with similar definitions are; dormancy induction (pre-dormancy), endodormancy or dormancy (true dormancy), and ecodormancy or quiescence (post-dormancy).

Buds are considered to break dormancy when exposed to “chilling” temperatures between -5 to 10°C for a period of time (e.g. Cannell & Smith, 1983), but due to lack of visible signs of dormancy release is physiological chilling requirement difficult to quantify (Linkosalo *et al.*, 2008). For species with a low chilling requirement, such as birch and Norway spruce, true dormancy could be broken already in late autumn or early winter (Hannerz *et al.*, 2003). The chilling requirement depend on local adaptation to prevent an early growth onset, minimising the risk for frost damage (Cannell & Smith, 1983), but is also influenced by temperature during dormancy induction, with higher temperatures deepening the bud dormancy and thus increase the chilling requirement (Heide, 2003, Sjøgaard *et al.*, 2008).

Budburst

About one third of the carbon stored from the previous growing season is used during flushing (Larcher, 2003), which from budburst to leaves with full photosynthetic capacity can take up to 70 days for oak (Morecroft *et al.*, 2003).

After break of true dormancy, warmer and longer days promote ontogenetic development towards budburst. In northern Europe, chilling requirement is assumed to commonly be met during autumn, and thus can higher winter and spring temperatures promote earlier leaf out (Menzel & Sparks, 2006, Myking & Heide, 1995). In contrast, in southern and coastal Europe where autumns and winters are commonly mild, warm winters can lead to inadequate dormancy release and delayed budburst (Cannell & Smith, 1986). However, there are indications that long days can compensate for insufficient chilling (e.g. Caffarra &

Donnelly, 2011, Heide, 1993b) and the period of most influence to timing of budburst extend one to three months prior to budburst when the tree experience “forcing” temperatures (Fu *et al.*, 2012, Menzel, 2003). Budburst occur after a period with forcing temperatures, when the forcing requirement is met. Studies have shown that forcing requirement vary among species and among provenances (Hannerz *et al.*, 2003). In general, southern Norway spruce provenances have higher forcing requirements than northern provenances, which is an adaptation to slower seasonal transitions and higher risk of spring frost in central and eastern Europe compared with northern Europe (Hannerz, 1994). Long photoperiods (Heide, 1993a) or long exposure to chilling temperatures (Cannell & Smith, 1983) can reduce the forcing requirement, or enhance the forcing rate (Caffarra *et al.*, 2011), but there are indications that that photoperiod is only effective when buds are un-sufficiently chilling (Myking & Heide, 1995).

Phenology model theory

Phenology models have mainly been developed to capture processes of a few trees, often of a few species using short time-series. They vary in their complexity and plant physiological realism, but cannot be considered truly process-based (Richardson *et al.*, 2013). Temperature is in the models calculated to temperature sums (or equivalent), with chilling temperatures below and forcing temperatures above a base temperature. Daily temperature sum is accumulated until a threshold or a requirement is exceeded. The following sections give an overview of how models represent trees response to temperature and photoperiod.

Budburst models

The theory of chilling is often based on the trees response around an optimum temperature (Fig. 4), thus too high or too low temperatures will in the model not contribute to the chilling accumulation. The state of chilling determines the models response to forcing temperatures, often described through a competence function (Fig. 5). The competence reflects if the possibility to accumulate chilling and forcing is considered separate in time or parallel, and ranges from 0 to 1. For models that consider chilling and forcing sequential, forcing will not accumulate until the chilling requirement is met. Parallel accumulation include e.g. the perception of deepening and decreasing rest during which the window for forcing accumulation becomes smaller and larger around a chilling threshold, respectively. Another model divides the chilling period into three phases; pre-rest, true rest and post-rest with no competence during true rest and with full competence during pre- and post-rest.

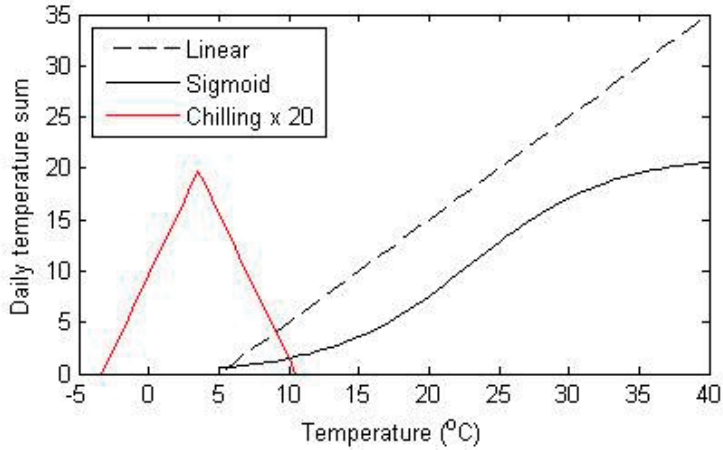


Figure 4. Example of chilling and forcing temperature response, with temperature thresholds; $T_{min}=-3.5^{\circ}C$, $T_{opt}=3.5^{\circ}C$ and $T_{max}=10.5^{\circ}C$ for chilling and $T_b=5^{\circ}C$ for forcing.

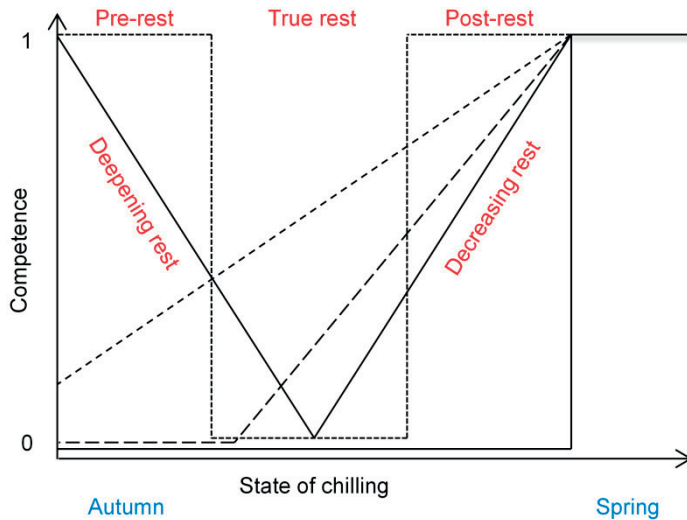


Figure 5. Example of some competence functions used in the models for ontogenetic development, and the perceived phases of dormancy (rest). Competence of 0 assumes no response to forcing temperatures and competence of 1 assumes full response to forcing temperatures. Each break-point in state of chilling indicates a chilling requirement.

Some models do only consider forcing, thus assumes that requirements in chilling and photoperiod is fully met. Forcing is often considered a linear or sigmoidal function of temperature (Fig. 3). Photoperiod can in the models be included as a starting day, or by modifying the temperature response, e.g. enhancing the forcing effect when days are longer. The forcing requirement is in most models fixed between years (e.g. the GDD model, Table 2), and is in a few models determined by climate conditions (e.g. Alternating model), with the amount of required forcing exponentially lowered for each additional chilling day.

Leaf colouring models

Comparatively fewer models have been developed for autumn phenology than for spring phenology. The structure of current leaf colouring models resemble that of the simpler budburst models, commonly considering a linear temperature response for temperatures under a base temperature, with the effect enhanced by either short or long days. No model includes a chilling requirement influenced by climate.

Aims and objectives

This thesis is part of a research project with the overall aim to estimate the impact of climate change on forest phenology, focusing on five tree species that are important in Swedish forest management; birch, beech, oak, Norway spruce and Scots pine.

The main aims and objectives of this thesis are to:

- Evaluate models ability to capture inter-annual and spatial variation in phenology (Paper I-IV).
- Discuss models representation of tree physiology processes (Paper IV).
- Assess and discuss uncertainties in phenological simulations in relation to;
 - Model structure (Paper I, III and IV)
 - Model calibration (Paper II and III)
 - Phenology data (Paper II)
 - Temperature data (Paper I and II)

Material and methods

Phenology data

The thesis focuses on five tree species most important in Swedish forestry and among the most important tree species in Europe; silver birch (*Betula pendula*), European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*).

Definition and data sets

Observations of day of budburst and leaf colouring of individual trees were used in Sweden, Austria, Finland, Germany and the United Kingdom, and were provided by the members of the Pan European Phenology project (PEP725), the Swedish Phenological network (SWE-NPN), and by the Swedish University of Agricultural Sciences (SLU) (Table 1).

The bulk of data consist of manual observations made by volunteers, thus to varying degree subjective. In general, observers are encouraged to select a tree within five kilometres from their home or workplace to motivate and facilitate frequent visits (Koch et al., 2009). The tree should be within a forest stand that is not located in an area with known climatic extremes, and represent the phenology of the stand. Of the data sets used, PEP725 is most extensive, with many trees observed for more than 30 years. The strength of the data lies in the number of observation sites and the long time-series, which generate spatial coverage and the possibility to assess model accuracy over time, linking it to changes in the climate. Information on tree age, height and provenance was not included in the data set.

The phenological observations are in PEP725 classified according to the BBCH-scale that identifies developmental stages and sub-phases of plants (Meier, 2001). The BBCH-scale was used as a benchmark when the definitions in the SWE-NPN and SLU data sets differed. Day of budburst was for deciduous trees defined as leaf unfolding on the first visible leaf stalk (BBCH 11) and for conifer trees defined as first leaves separated (BBCH 10). Day of leaf colouring was defined as when 50% of the leaves have shifted to autumn colours (BBCH 94).

Table 1. Summary of the data used in Paper I-IV. Scots pine was only included in Paper I due to few observations available.

Paper	Country	Species	Time period	Phase	Phenology data	Climate data
I	Sweden	Oak	1873-1918	Budburst	SLU PEP725 SWE-NPN	E-OBS 0.22° Station (SMHI)
		Birch				
		Beech				
		Scots pine				
		Norway spruce	1966-2011			
II	Germany	Birch	1951-1978	Budburst	PEP725	E-OBS 0.22° E-OBS 0.44° Station (E-OBS)
III	Austria					
	Finland	Birch	1951-2011	Budburst	PEP725	E-OBS 0.22°
	Germany	Norway spruce				
	United Kingdom					
IV	Austria	Oak				
	Germany	Birch	1951-2011	Leaf colouring	PEP725	E-OBS 0.22°
	United Kingdom	Beech				

Climate data

The phenology models were driven by observed daily mean air temperature. Three different spatial resolutions of observed temperature were used; the European E-OBS dataset with temperature interpolated to 0.44° (~50x50 km) and 0.22° (~25x25 km) (Haylock *et al.*, 2008), and temperature from meteorological stations underlying the interpolation of the E-OBS dataset (Klein Tank *et al.*, 2002) (Table 1). In addition, local temperature was approximated by adjusting station and gridded temperature using elevation differences and temperature lapse rate.

The E-OBS dataset are from 1950 to present. For historical simulations in Sweden, historical temperature was reconstructed using the E-OBS dataset to assess spatial and temporal differences in relation to temperature of eleven meteorological stations of the Swedish Meteorological and Hydrological Institute (SMHI).

Phenology models

The phenology models evaluated in this thesis ranges from being strictly empirical to intermediate empirical and mechanistic. The empirical models were based on linear regression with monthly temperature as the predictor. Table 2 give an overview of the models used. Some of the models are described in the Supporting information in Paper I, III and IV.

Model calibration and evaluation

Model calibration or parameterisation is the procedure to fit or tune a model to the phenological variation and climate conditions of interest, i.e. to location, time period and species. In general, more parameters increase the risk of over fitting the model and increase the models uncertainty by accumulating inherent uncertainty of the parameters (Dose & Menzel, 2004). Therefore should, according to Ockham's razor, simpler models be favoured over more complex models, unless the more complex model has a significantly higher degree of explanation. One example of model selection method is the Akaike's information criterion (AIC) that weights the goodness of fit against the complexity of the model.

Models are traditionally evaluated by comparing simulated and observed phenology, e.g. by using coefficient of determination (R^2), root mean square error (RMSE) and model bias, with positive bias indicating that phenology was simulated too late in relation to observed phenology. Pearson's correlation (r) was used to indicate trends, e.g. if bias was related to temperature, potentially indicating models that would provide less reliable predictions in a warmer climate.

It is essential to evaluate the models with external data, since the better fitted models can perform the worst when evaluated at sites not included in the calibration (Chuine *et al.*, 1998). The models were in Paper II and III evaluated using the observations not included in the calibration, whereas all observations were included in both the calibration and evaluation in Paper IV. Different evaluation methods were used in Paper I since timing of budburst was not simulated. The models were instead evaluated based on the relative variation in model state, i.e. amount of accumulated temperature sum, at day of phenological event, which indicate what the forcing requirement should have been for a specific year and tree. The gradients in forcing requirement were related to latitude, temperature and thermal continentality.

Table 2. Overview of the models used in Paper I-IV, the different names used and suggested references. In Paper IV, 34 composed models were compared in addition to DM and GSI, but only the four models with references are shown.

Model	Paper I	Paper II	Paper III	Paper IV	Reference
Mean $T_{\text{Feb-Apr}}$			Mean $T_{\text{Feb-Apr}}$		-
Average day	M1				Kramer (1994)
Thermal time	M2	GDD	GDD ₁	GDD _{LIN}	Cannell & Smith (1983)
			GDD _{DOY}		Cannell & Smith (1983)
			GDD _{CON}		-
			GDD _{FROST}		-
Sequential	M3		SEQ		Hänninen (1990)
Parallel	M4				Hänninen (1990)
Deepening rest	M5				Hänninen (1990)
Four phase	M6				Hänninen (1990)
Synthesis	M7				Hänninen (1990)
Alternating	M8		ALT		Cannell & Smith (1983)
UniForc	M9				Chuine (2000)
UniChill	M10				Chuine (2000)
Unified	M11				Chuine (2000)
DORMPHOT	M12		DORMPHOT		Caffarra et al. (2011)
ForcSar	M13		SIG	GDD _{SIG}	Chuine et al. (1999)
2D-3C-4A	M14				Hänninen (1995)
PIM 11	M15		PIM		Schaber & Badeck (2003)
BC		BC	BC		Blümel & Chmielewski (2012)
DM				DM	Delpierre et al. (2009)
Growing season index				GSI	Jolly et al. (2005)
Model 3				CDD _{LIN}	Richardson et al. (2006)
Model 4				GDD _{LIN} CDD _{LIN}	Richardson et al. (2006)

Results and discussion

Models are evaluated based on how well they meet user demands for accuracy, which depends on context and aim of the study. Phenology models that are incorporated in ecosystem models are commonly simple and general, focusing on capturing large-scale vegetation patterns of many different tree species (Smith *et al.*, 2001, Wallman *et al.*, 2005). It has been shown for a beech forest in eastern France, that the uncertainty in simulated daily and annual net ecosystem exchange (NEE) that was related to the temperature sum requirement, was about five times higher for leaf fall than for budburst (22.2 and 4.1%) (Dufrêne *et al.*, 2005).

Phenology models have mainly been developed to capture processes of a few trees, often using short time-series. In this thesis, phenology models were evaluated based on their ability to capture inter-annual and large-scale spatial variation in budburst and leaf colouring. The simulations were assessed in relation to model structure, i.e. the models representation of trees response to temperature and photoperiod, and the calibration -, phenology – and temperature data used.

The models structure influence the models sensitivity to calibration data and climate conditions

Temperature is the main driver of all phenology models tested in this thesis. Models ability to capture the temperature effect was found to mainly be influenced by model structure (Paper I, III, IV), which is in accordance with previous studies (Migliavacca *et al.*, 2012). The relation between phenology and environmental cues varying among scales (Pau *et al.*, 2011), and the models ability to estimate the temperature effect vary between inter-annual variations at individual sites and spatial variations (Paper II, III). Overall, most budburst models overestimated the temperature effect (Paper III). In colder regions where budburst usually occurs later, budburst was simulated to occur too late, and in warmer regions where budburst occurs earlier, budburst was simulated to occur too early. Most leaf colouring models underestimated the temperature effect, however, average day of leaf colouring provided a better estimate than the simulations (Paper IV). The

structure of the more accurate leaf colouring models were reduced to counting number of days from summer solstice.

It is appealing to assume that more complex models are more physiologically realistic and thus more accurate than simpler models. Simpler models are however often more general and therefore more able to estimate the relationship between temperature and phenology at a larger scale. In Paper I and III, it was shown that more complex budburst models often are less accurate, which is in line with previous studies on local phenology (Chuine *et al.*, 1998, Fu *et al.*, 2012, Häkkinen *et al.*, 1998, Hannerz, 1999, Hunter & Lechowicz, 1992, Richardson & O'Keefe, 2009). In general, budburst models that were more sensitive to temperature conditions included features like; i) upper and lower chilling temperature thresholds, thus no response to temperatures higher or lower than the thresholds, ii) one or more fixed chilling requirements, especially in combination with sequential phases that imply no response to forcing temperatures unless dormancy is fully broken, and iii) response to forcing temperatures before dormancy induction and release (Paper I).

The more accurate budburst and leaf colouring models assumed a linear response to temperatures above and below a base temperature, respectively, instead of a sigmoidal response. For leaf colouring, the temperature response was enhanced by shorter days, and for budburst was the temperature response enhanced by longer days for one of the better models (Paper III, IV).

With more complex models in general having more parameters, the results are influenced by the accumulated uncertainty of each parameter. The more accurate budburst models include the effect of forcing temperatures, thereby assuming full dormancy release without considering chilling temperatures. If chilling requirements are met already in late autumn or early winter (Hannerz *et al.*, 2003), it implies that additional chilling only has little effect and that the importance of a chilling component in is reduced for simulations in current climate. This makes the models representation of winter dormancy more difficult to evaluate.

Fixed and dynamic requirements

The models tested in the thesis vary in complexity, but have mainly been developed to capture the processes of individual trees, and are less able to capture phenological differences among trees (Chuine, 2000, Chuine *et al.*, 1998, Hanes & Schwartz, 2011). Studies imply that chilling and forcing requirement for budburst vary among provenances, in general lower forcing requirements for more northern provenances (Hannerz, 1994, Hannerz *et al.*, 2003). Chilling requirements are difficult to quantify since the attainment lack visible signs, relative to forcing requirement which is observed through bud development. Provenance trials that estimate provenance-specific forcing requirements often overlook the interaction

of photoperiod, chilling and forcing, by only calculating temperature sums till budburst. Therefore, the estimated forcing requirement also includes the transfer effect in relation to provenance-specific requirements in chilling and photoperiod.

Most budburst models and all leaf colouring models include a temporally and spatially fixed forcing requirement, and thus rely on the model structure to capture the environmental response in a way that enables using a fixed requirement. When calibrated at different sites the modelled requirement represent a provenance-specific requirement. Models with a dynamic forcing requirement assumes no provenance-specific requirement since the modelled forcing requirement is determined by number of chilling days, and local adaptation is only inferred in the negative exponential function that describes the relation.

Extracting accumulated temperature sum at day of budburst of leaf colouring showed that the modelled requirement varied spatially and in time when other variables are kept constant (Fig. 6, Paper I, IV), which is in accordance with previous studies (Fisher *et al.*, 2007, Gunderson *et al.*, 2012). This is in support for requirements that are influenced by prior conditions, such as in the Alternating model. However, in Paper I it was shown that only 53% or less of the variation in forcing requirement was explained by number of chilling days.

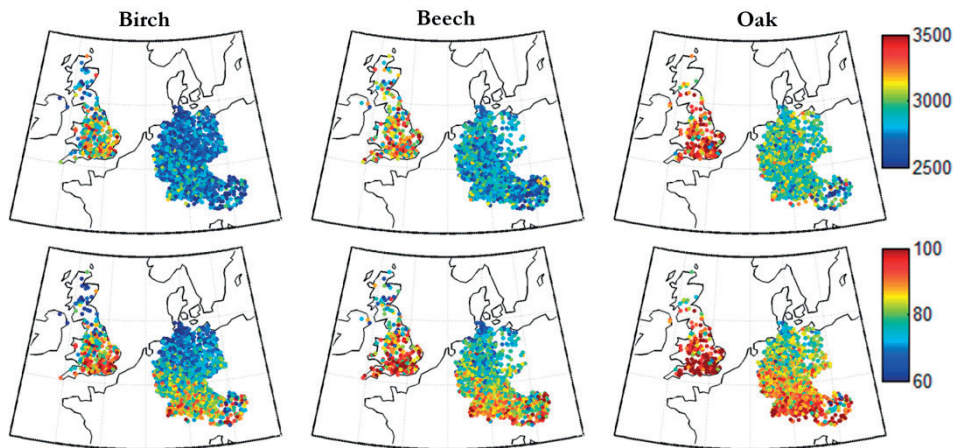


Figure 6. Modelled site-specific temperature sum requirement for two leaf colouring models; CDD_{LIN,DL} (upper row) and DM₁ (lower row). The models were among the better performing models, with DM₁ basically counting number of days till day of leaf colouring. Figure adapted from Paper IV.

The calibration data influence model accuracy

It is desirable that parameter values are physiological meaningful, such as the starting day for temperature sum accumulation potentially indicating a photoperiod requirement. However, this is not always the case. For example, no photoperiod requirement was implied for leaf colouring since any day within a period of weeks would have generated similar results (Paper IV).

Parameters are interdependent, as shown for the growing degree-day model that includes a starting day, base temperature and forcing requirement (Paper III, Fig. 7). If using an earlier starting day and lower base temperature, more days will influence the forcing accumulation and result in greater variation in simulated day of budburst, than if using a later starting day and a higher base temperature. For simulations in a warmer climate with models that do not consider chilling, the starting day defines the limit for advancement. Using an early starting day could result in unrealistic predictions when it is too dark for trees to flush.

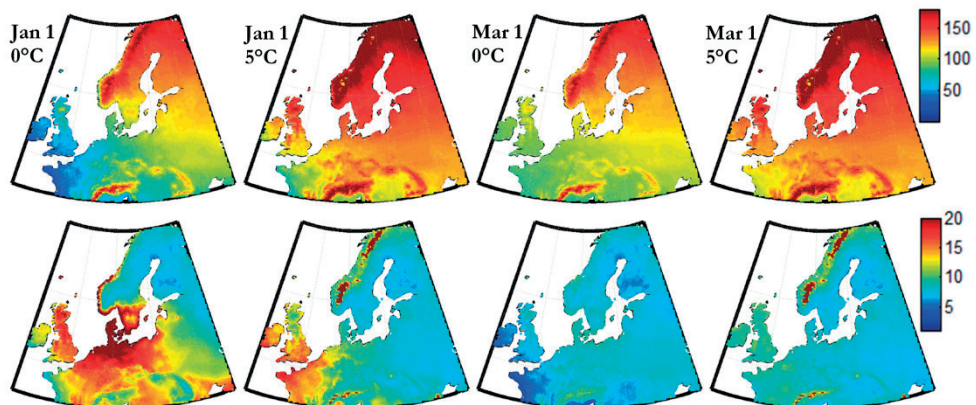


Figure 7. Variation in forcing in relation to starting date (January 1 or March 1) and base temperature (0 or 5°C) using the growing degree-day model (GDD). Upper row shows the mean day when accumulated forcing of 200 is reached between 1950 and 2012, with lower row showing the standard deviation. Figure adapted from Paper III.

Since all models contain empirical components that need to be calibrated, the performance depends to varying degree on the calibration data (Paper II, III). Through the calibration, the models are tuned to the average phenological response of the calibration data. With the bulk of data used from Germany, the accuracy of the simulations in Austria, Finland and the United Kingdom was influenced by the relative difference to the conditions in Germany (Paper III, IV). For example, budburst was simulated to occur too early in the United Kingdom and too late in Finland. This was partly explained by an overestimation of the

temperature effect and partly by higher and lower temperatures, respectively, in relation to temperatures Germany. The calibrated forcing requirement would therefore be met earlier in the United Kingdom and later in Finland, unless the forcing accumulation was restrained by chilling or photoperiod. Models tested in Paper III were with few exceptions on average across the whole study region simulating later than observed budburst with higher spring temperatures (Fig. 8).

Using many trees enables a better representation of the regional average and thus better regional model accuracy, and overall were the more complex models more sensitive to differences in calibration data (Fig. 8 (right panel), Paper III). With The regional accuracy of model simulations based on a single site varied depending on the calibration site (Paper II, III). At the calibration site Bad Lippspringe in Germany, two models were fitted better than at Saarbrücken/Ensh, but the calibration that was generated at Bad Lippspringe did not extrapolate well to Saarbrücken/Ensh (Paper II). When using both sites in the calibration it was apparent that Bad Lippspringe influenced the calibration the most.

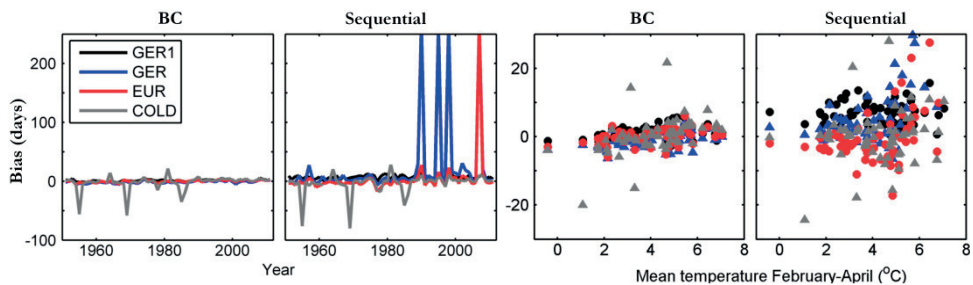


Figure 8. Average regional model bias for birch using two budburst models, BC and the more complex Sequential, and four different calibration schemes; GER1 (one site in Germany), GER (multiple sites in Germany), EUR (10 sites each in Austria, Finland, Germany and the United Kingdom) and COLD (all site-years classified as cold). Bias in relation to year (left) and to mean temperature February-April for each year. Negative bias indicate that budburst on average was simulated to occur before observed budburst. Figure adapted from Paper III.

Temperature and phenology data

An advantage of using gridded temperature data as in this thesis is that time-series of phenological observations that are not close to a meteorological station can be included in model development. In Paper II, different spatial resolutions of temperature data sets were used; observed temperature from a nearby meteorological station, gridded temperature, and observed and gridded temperature adjusted to the location of the tree. The results indicated that the spatial resolution of temperature influence model accuracy at individual sites, but the result varied greatly among sites. Overall was 44° grid-cell temperature too different from the local temperature, and adjusting the temperature was at some

sites insufficient to improve the simulations. Using 0.22° gridded temperature generated comparable results as when using station temperature, which indicate that relatively reliable comprehensive simulations can be achieved. When evaluating the regional model performance, the use of phenology grid-cell averages may provide more representative estimates than the use of individual observations when using gridded temperature.

The phenology data used to calibrate and evaluate the models are associated with uncertainty related to e.g. observer subjectivity and unknown provenance. When provenance is not known, spatial variation in phenology is assumed to be the effect of local variations in temperature conditions (Chen, 2013). However, if the genetic variation is not correlated with climate, it will make models even more difficult to calibrate (Richardson *et al.*, 2006). It is estimated that the genetic variation in birch, Norway spruce and Scots pine is greater within than among populations (Mátyás *et al.*, 2004, Vakkari, 2009). This implies that model accuracy can vary between trees that are located close to each other and assumed to be under the influence of the same climate, as was shown in Paper II.

In the 1960s, a network of International Phenological Gardens (IPGs) was established in Europe with clones of various species, thereby removing the genetic variation (Chuine *et al.*, 2000, Sparks & Menzel, 2002). However, without knowing the requirements of locally adapted trees, quantifying the effect of provenance transfer and plasticity remains difficult, especially as the response also varies among clones (Box 1).

Provenance transfers

Provenance transfers since the 1850's has created artificial forests of Norway spruce in Scandinavia and Central Europe (Skrøppa, 2003). Provenance and cultivation research to find desirable traits is comprehensive for commercially important species, and some provenances have been identified as having superior growth characteristics, such as better stem form, or herbivore resistance.

The majority of Norway spruce provenances used in southern Scandinavia are mostly from Central and East Central Europe (Langlet, 1960), and in Germany and the United Kingdom from Poland and Rumania (Lieseback *et al.*, 2010). Planting of trees within and outside species natural range influence the spatial variation in adaptive traits like phenology. In general is the spatial variation for Norway spruce and Scots less distinct in Central than in Northern Europe due to the long history of planting (Mátyás *et al.*, 2004, Skrøppa, 2003). Provenance transfers are however not without risk. For example, birch provenances are not recommended to be transferred more than 150 km north or south from its origin in Finland, due to the increased risk of damage by late spring and early autumn frost. In Central Europe where the adaptation along bioclimatic gradients is less strong, provenances can be transferred longer distances (Vakkari, 2009).

Box 1. Differences in temperature response among clones

The Forestry Research Institute of Sweden (Skogforsk) engages in research on e.g. tree breeding and forest management. In 2010, Skogforsk initiated an experiment at Ekebo on Norway spruce, exposing ten clones of different provenances to four different treatments with elevated temperatures. Shoot development of lateral buds were recorded in spring 2011, with budburst defined as the day when bud scales had separated and green needles were visible (Johan Westin, personal communication).

In the experiment, between four to seven copies of each clone with seed origins from selected trees growing in Sweden, but with parental origin in Romania (provenance; Brosteni, Ilva Mica or Moldovita), Poland (Istebna) or Sweden (Trolleholm or Tunbyholm), were used. The plants were treated with temperatures regulated to ca. 5 or 15°C; continuously (w. 39-13, C), in autumn (w. 39-42, A), in winter (w. 51-2, W) and in spring (w. 10-13, S). Before treatments, plants were transferred to the greenhouse for a short transitions period to reduce stress. When not in the greenhouse, the plants were kept outdoors with the control (w. 35-13, Control). Light conditions were not regulated.

With permission from Skogforsk, I analysed treatment effects and differences among clones using an univariate ANOVA on all plants (significance at $p < 0.05$). Clones responded significantly different to treatments, and treatments had a significant impact on timing of budburst, with a significant interaction between clones and treatments. Budburst occurred significantly earlier with elevated spring temperatures; ca. 15-20 days earlier than with continuous treatment, and ca. 35 days earlier than with the other autumn and winter treatments (Fig. B1a). The results imply that plants are more responsive to spring temperatures, with a higher effect if winters are sufficiently cold. Delayed or less advanced budburst could indicate a late break of winter rest due to high winter temperatures relative to the chilling requirement that might vary among clones (e.g. 15 W in Fig. B1b).

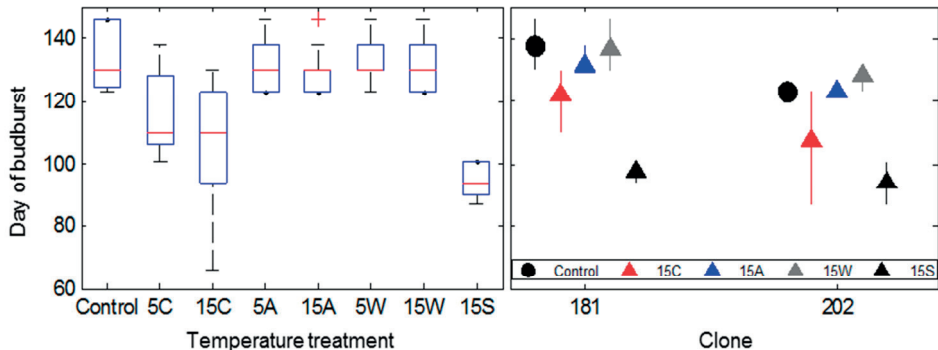


Figure B1. Boxplot of the response to elevated temperature by ten Norway spruce clones with four to seven plants per clone and trial (5°C or 15°C during autumn (A), winter (W), spring (S) or continuous (C)). Right figure show the average temperature response (and range) of 15°C treatment for two clones that share genetic line two generations back.

Models simplify physiological processes

Phenology models have often been developed based on knowledge attained from experimental studies, mainly carried out on juvenile trees that may have a stronger temperature response than mature trees (Partanen *et al.*, 2005, Vitasse, 2013). It was recently shown that using cuttings harvested after dormancy instead of juvenile trees makes a better proxy of mature trees phenological response to temperature (Vitasse & Basler, 2013). Experimental studies rarely capture the natural variation in temperature, and therefore do budburst models rarely include the impact of late spring frost that may reset ontogenetic development (Chuine *et al.*, 1999, Linkosalo *et al.*, 2006). Conclusions of experimental studies are influenced by the study design. It is difficult to infer what potentially delay or advance phenology when experimental results are based on e.g. fixed temperature treatments, with the definition of “warmer” and “colder” temperatures not related to a physiological temperature optimum. There are indications that the phenological response to temperature is fourfold underestimated compared to the response observed in nature (Wolkovich *et al.*, 2012).

Phenology models represent simplifications of our understanding of physiological processes. Data availability can limit the possibility to include other environmental factors than daily temperature and photoperiod, especially for climate scenarios and large-scale spatial simulations. The influence of e.g. water and nutrient availability is acknowledged but even less understood (Hudson, 2010).

Temperature and photoperiod

High light intensity has been shown to advance budburst in beech and birch (Caffarra & Donnelly, 2011). The bud can especially during spring experience a considerably higher temperature than the ambient air temperature due to intense solar radiation (e.g. Sarvas, 1972, in Hannerz, 1994).

There are indications that trees are more responsive to day or night temperatures. Experimental studies on poplar indicate that warmer nights accelerate growth cessation and dormancy development, whereas warmer days have the opposite effect (Kalcsits *et al.*, 2009). Fluctuating temperatures have been demonstrated to promote dormancy release and ontogenetic development more than constant temperatures, suggesting that biochemical processes with different temperature optimum are involved (Partanen *et al.*, 1998). However, the efficiency of fluctuating temperatures on promoting budburst may be influenced by chilling temperature, with no effect when chilling requirements are met (Myking, 1997).

It has been implied that changes in photoperiod are more influential than actual day length, with shortening photoperiod delaying budburst in Norway spruce for

several weeks when combined with fluctuating temperatures (Partanen *et al.*, 1998). Thus, shortening of photoperiod before winter solstice could prevent premature ontogenetic development when autumns are warm.

Water and nutrient availability

Norway spruce becomes photosynthetic activity when the soil thaws and water becomes available (Bergh *et al.*, 1998). During winter, tissues become dehydrated and water availability influence the bud swelling which can take one to three weeks, implying that low water availability could delay budburst (Laube *et al.*, 2014). Higher air humidity was shown to advance budburst in e.g. birch, oak and Norway spruce (Laube *et al.*, 2014). An increased amount of nutrients involved in changes in turgor pressure and cell extension can also advance budburst, such as potassium and calcium (but not nitrogen and phosphorus) (Jochner *et al.*, 2013).

High nitrogen content in the leaves can delay leaf senescence and the development of frost hardiness (Keskitalo *et al.*, 2005), while drought can induce leaf senescence (Lim *et al.*, 2007). In general, precipitation indices are not strong influential factors (Cufar *et al.*, 2012), with a few sites indicating earlier leaf colouring with dryer autumn months the year before (Estrella & Menzel, 2006). Drought is a complex phenomenon, influenced by soil type, slope and the combined effect of precipitation and temperature, making drought difficult to estimate from precipitation alone.

Models potential to predict future changes in phenology

The overall results indicate that the models do not capture the phenology across large regions, which emphasise the uncertainty in phenological processes, especially for leaf colouring. It is important that models capture extreme years that in the future could become the norm or at least become more common. Since the budburst models tend to overestimate, and the leaf colouring models underestimate the temperature effect (in addition to not being able to simulate leaf colouring more accurately than average day), it is unlikely that the models would make reliable predictions. As shown in this thesis, model structure influence the models sensitivity to temperature, and some models are more likely than others to make more reliable projections.

Temperature sensitivity of budburst models was evaluated in Paper I by adding -6 to 9°C, with steps of 3°C, to a historical temperature time-series from Lund (1875-1876). Taking into account the around 0.7°C temperature increase since 1875 to the reference period of 1986-2005, and that surface air temperature over land in

general is higher than the global mean with the RCP scenarios; the manipulated time-series correspond roughly to climate scenario RCP4.5 (+3°C) and RCP4.5 (+6°C) with -6, -3 and +9°C representing extreme years. Most budburst models simulated budburst earlier with temperatures +3 and +6°C, and later with -3°C (Fig. 9). With extreme temperatures (+9 or -6°C), winter temperatures were either too high or too low to meet the chilling requirements. In contrast, two models that incorporate forcing temperatures during autumn, simulated budburst already in November and December with the two warmest temperature time-series. For these models, using a later starting day for forcing accumulation during autumn prevented the forcing accumulation to be too early and too much, thus preventing budburst to be simulated too early. This highlights the difficulties of spatial modelling using fixed requirements that do not vary with bioclimatic- or provenance-specific gradients.

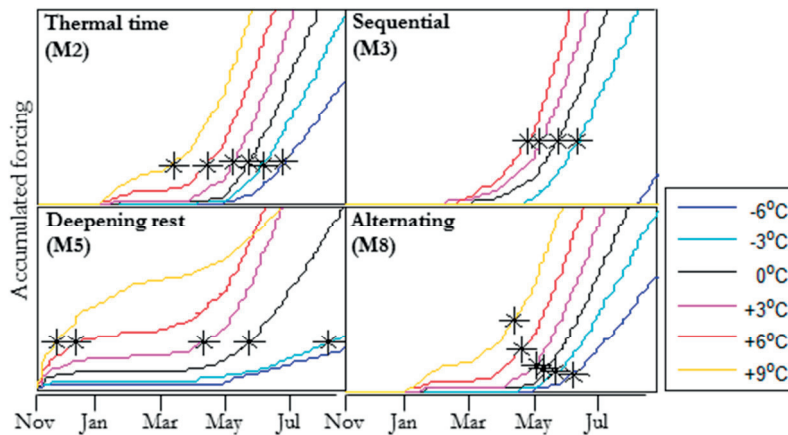


Figure 9. Temperature sensitivity of four budburst models, with a temperature time-series from Lund 1875-1876 modified by adding -6, -3, 0, 3, 6 and 9°C. Asterix indicate simulated day of budburst. Thermal time, Sequential and Deepening rest has a fixed forcing requirement while the Alternating model has a forcing requirement related to number of chilling days. Figure adapted from Paper I.

Substantial winter warming could lead to chilling deficit in regions where winters are commonly mild and for species with high chilling requirements (Vitasse & Basler, 2013). Delayed dormancy release can delay budburst, unless the chilling deficit is compensated by increased forcing or long days. While budburst models that include the effect of chilling temperatures potentially could capture a delay in dormancy release, they are in general not as accurate as simple forcing models in current climate (Paper I, III). Forcing models cannot account for delayed budburst due to insufficient chilling. Leaf colouring models have similar limitations; they cannot capture a prolongation in the growing season due to warm autumn days if considering temperatures above the base temperature since the temperature sum

requirement would be reached faster with higher temperatures. If the model considers temperature below the base temperature, which is commonly the case, leaf colouring can be simulated to occur at the latest when temperatures equals the base temperature, since higher temperatures do not contribute to the temperature sum accumulation.

The model bias of most budburst and leaf colouring models was significantly negatively related to priori average temperatures, indicating a more negative bias at warmer sites and for warmer years (Paper III, IV). This indicates that the budburst models simulated a stronger advancement than what was observed with higher temperatures in February-April (overestimated temperature effect), and that the leaf colouring models simulated a less prolongation of the growing season than observed with higher temperatures in April-August (underestimated temperature effect). Overall, models that in current climate are considered more reliable have an underlying theory that is not fully supported, while more complex models that can be considered more physiological realistic are not general enough to capture phenology in different climate conditions.

Conclusions

In this thesis, phenology models were assessed based on how well they capture inter-annual and spatial variation in phenology. None of the models developed and tested were able to simulate the phenology across large regions accurately enough to be considered reliable for use in climate change assessments. With temperature as the main driver, the overall low accuracy indicates that the temperature response is not well represented in the models, which emphasise the lack of mechanistic understanding of phenological processes.

The modelled response to inter-annual variations in temperature at individual sites did not support using a fixed requirement, and the models did not consider provenance-specific requirements. In the calibration, the models were tuned to the average phenological response. Model structure influenced the models sensitivity to the calibration data and to climate conditions, in general more so for the more complex models. Uncertainties in model structure were therefore concluded to be of more importance than uncertainties in phenology and climate data.

Most budburst models overestimated the temperature effect. They simulated budburst too late in colder regions where budburst in general occur later, and too early in warmer regions where budburst occur earlier. The more accurate budburst models assumed full dormancy release without considering winter conditions. They assumed a linear response to forcing temperatures, some with the response enhanced by longer days and some with the forcing requirement lowered for each additional chilling day. On contrary, most leaf colouring models underestimated the temperature effect, which is in line with that average day of leaf colouring provided a better estimate than the simulations. This emphasise the greater uncertainty associated with autumn phenology than with spring phenology. The more accurate leaf colouring models assumed a linear response to temperature, starting at summer solstice and with shorter days having a small enhancing effect.

The models differed in accuracy among species, but overall were the same models better for most species. This supports the usage of only one phenology model with parameter values specific to species or plant functional types in ecosystem models.

Outlook

The results highlight the difficult task to develop and select a phenology model that makes reliable predictions across large regions and that can be used in climate change impact assessments. Further research is needed on trees response to environmental cues, especially on the interaction between temperature and photoperiod throughout the year, and how the response varies among trees within and among populations. To overcome some of the uncertainties in the phenology data, trees with known provenance could be used. More stages than just day of budburst or leaf colouring could be considered to assure that the models capture the phenological processes of flushing and leaf senescence. This would better link phenology to e.g. trees photosynthetic activity, and could bring ground observed phenology closer to remotely sensed phenology; two aspects of phenology to be used when developing models.

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References

- Ahas R, Aasa A, Menzel A, Fedotova VG, Scheifinger H (2002) Changes in European spring phenology. *International Journal of Climatology*, **22**, 1727-1738.
- Archetti M, Richardson AD, O'Keefe J, Delpierre N (2013) Predicting Climate Change Impacts on the Amount and Duration of Autumn Colors in a New England Forest. *PLOS ONE*, **8**, 1-9.
- Bergh J, Mcmurtrie RE, Linder S (1998) Climatic factors controlling the productivity of Norway spruce: A model-based analysis. *Forest Ecology and Management*, **110**, 127-139.
- Blümel K, Chmielewski F-M (2012) Shortcomings of classical phenological forcing models and a way to overcome them. *Agricultural and Forest Meteorology*, **164**, 10-19.
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625-644.
- Caffarra A, Donnelly A (2011) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International Journal of Biometeorology*, **55**, 711-721.
- Caffarra A, Donnelly A, Chuine I (2011) Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research*, **46**, 159-170.
- Cannell MGR, Smith RI (1983) Thermal Time, Chill Days and Prediction of Budburst in *Picea sitchensis*. *Journal of Applied Ecology*, **20**, 951-963.
- Cannell MGR, Smith RI (1986) Climatic Warming, Spring Budburst and Forest Damage on Trees. *Journal of Applied Ecology*, **23**, 177-191.
- Chuine I (2000) A Unified Model for Budburst of Trees. *Journal of Theoretical Biology*, **207**, 337-347.
- Chuine I, Beaubien EG. (2001) Phenology is a major determinant of tree species range. *Ecology Letters*, **4**, 500-510.
- Chuine I, Belmonte J, Mignot A (2000) A Modelling Analysis of the Genetic Variation of Phenology between Tree Populations. *Journal of Ecology*, **88**, 561-570.
- Chuine I, Cour P, Rousseau DD (1998) Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell and Environment*, **21**, 455-466.
- Chuine I, Cour P, Rousseau DD (1999) Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling. *Plant, Cell and Environment*, **22**, 1-13.
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, **22**, 357-365.

- Cufar K, Luis M, Saz M, Crepinsek Z, Kajfez-Bogataj L (2012) Temporal shifts in leaf phenology of beech (*Fagus sylvatica*) depend on elevation. *Trees*, **26**, 1091-1100.
- Delpierre N, Dufrene E, Soudani K, Ulrich E, Cecchini S, Boe J, Francois C (2009) Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. *Agricultural and Forest Meteorology*, **149**, 938-948.
- Dose V, Menzel A (2004) Bayesian analysis of climate change impacts in phenology. *Global Change Biology*, **10**, 259-272.
- Dufrêne E, Davi H, Francois C, Maire GI, Dantec VI, Granier A (2005) Modelling carbon and water cycles in a beech forest: Part I: Model description and uncertainty analysis on modelled NEE. *Ecological Modelling*, **185**, 407-436.
- ECA&D, European Climate Assessment & Dataset. Accessed 2014-05-21 at <http://eca.knmi.nl/FAQ/index.php>
- Estrella N, Menzel A (2006) Responses of leaf colouring in four deciduous tree species to climate and weather in Germany. *Climate Research*, **32**, 253-267.
- Fisher JJ, Richardson AD, Mustard JF (2007) Phenology model from surface meteorology does not capture satellite-based greenup estimations. *Global Change Biology*, **13**, 707-721.
- Fitter AH, Fitter RSR (2002) Rapid Changes in Flowering Time in British Plants. *Science*, **296**, 1689-1691.
- Fu YH, Campioli M, Van Oijen M, Deckmyn G, Janssens IA (2012) Bayesian comparison of six different temperature-based budburst models for four temperate tree species. *Ecological Modelling*, **230**, 92-100.
- Gunderson CA, Edwards NT, Walker AV, O'hara KH, Champion CM, Hanson PJ (2012) Forest phenology and a warmer climate - growing season extension in relation to climatic provenance. *Global Change Biology*, **18**, 2008-2025.
- Häkkinen R, Linkosalo T, Hari P (1998) Effects of Dormancy and Environmental Factors on Timing of Bud Burst in *Betula Pendula*. *Tree Physiology*, **18**, 707-712.
- Hanes JM, Schwartz MD (2011) Modeling land surface phenology in a mixed temperate forest using MODIS measurements of leaf area index and land surface temperature. *Theoretical and Applied Climatology*, **105**, 37-50.
- Hannerz M (1994) Predicting the Risk of Frost Occurrence after Budburst of Norway Spruce in Sweden. *Silva Fennica*, **28**, 243-249.
- Hannerz M (1999) Evaluation of temperate models for predicting bud burst in Norway spruce. *Canadian Journal of Forest Research*, **29**, 9-19.
- Hannerz M, Ekberg I, Norell L (2003) Variation in Chilling Requirements for Completing Bud Rest Between Provenances of Norway Spruce. *Silvae Genetica*, **52**, 161-168.
- Hänninen H (1990) Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica*, **213**, 1-47.
- Hänninen, H., 1995. Effects of climate change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. *Canadian Journal of Botany*, **73**:183-199.
- Hänninen H, Kramer K (2007) A Framework for Modelling the Annual Cycle of Trees in Boreal and Temperate Regions. *Silva Fennica*, **41**, 167-205.
- Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M (2008) A European daily high-resolution gridded dataset of surface temperature and precipitation. *Journal of Geophysical Research*, **113**, 1-12.
- Heide OM (1993a) Daylength and thermal time responses of budburst during dormancy in some northern deciduous trees. *Physiologia Plantarum*, **88**, 531-540.

- Heide OM (1993b) Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum*, **89**, 187-191.
- Heide OM (2003) High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climate warming. *Tree Physiology*, **23**, 931-936.
- Hudson II (2010) Interdisciplinary approaches: towards new statistical methods for phenological studies. *Climatic Change*, **100**, 143-171.
- Hunter AF., Lechowicz MJ. (1992) Predicting the timing of budburst in temperate trees. *Journal of Applied Ecology*, **29**, 597-604.
- Ibáñez I, Primack RB, Miller-Rushing AJ *et al.* (2010) Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society*, **365**, 3247-3260.
- Isaacson BN, Serbin SP, Townsend PA (2012) Detection of relative differences in phenology of forest species using Landsat and MODIS. *Landscape Ecology*, **27**, 529-543.
- Jeong S-J, Medvigy D, Shevliakova E, Malyshev S (2012) Uncertainties in terrestrial carbon budgets related to spring phenology. *Journal of Geophysical Research-Biogeosciences*, **117**, 1-17.
- Jin H, Eklundh L (2014) A physically based vegetation index for improved monitoring of plant phenology. *Remote Sensing of Environment*, **152**, 512-525.
- Jochner S, Höfler J, Beck I, Göttlein A, Ankerst DP, Traidl-Hoffmann C, Menzel A (2013) Nutrient status: a missing factor in phenological and pollen research? *Journal of Experimental Botany*, **64**, 2081-2092.
- Jolly WM, Nemani R, Running SW (2005) A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology*, **11**, 619-632.
- Jönsson AM, Barring L (2011) Ensemble analysis of frost damage on vegetation caused by spring backlashes in a warmer Europe. *Natural Hazards and Earth System Sciences*, **11**, 401-418.
- Jönsson AM, Lagergren F, Smith B (2013) Forest management facing climate change - an ecosystem model analysis of adaptation strategies. *Mitigation and Adaptation Strategies for Global Change*, 1-20.
- Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B (2012) Guess the impact of *Ips typographus* - an ecosystem modelling approach for simulating spruce bark beetle outbreaks. *Agricultural and Forest Meteorology*, **166-167**, 188-200.
- Junttila O, Nilsen J, Igeland B (2003) Effect of Temperature on the Induction of Bud Dormancy in Ecotypes of *Betula pubescens* and *Betula pendula*. *Scandinavian Journal of Forest Research*, **18**, 208-217.
- Kalcsits La, Silim S, Tanino K (2009) Warm temperature accelerates short photoperiod-induced growth cessation and dormancy induction in hybrid poplar (*Populus x spp*). *Trees*, **23**, 971-979.
- Keenan TF, Gray J, Friedl MA *et al.* (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Clim. Change*, **4**, 598-604.
- Keskitalo J, Bergquist G, Gardeström P, Jansson S (2005) A Cellular Timetable of autumn Senescence. *Plant Physiology*, **139**, 1635-1648.
- Kikuzawa K (2004) Ecology of Leaf Senescence. In: *Plant Cell Death Processes*. (ed Noodén L, D.) pp Page. San Diego, Academic Press.
- Klein Tank AMG, Wijngaard Jb, Können GP *et al.* (2002) Daily dataset of 20th-century surface air temperature and precipitation series for the European climate assessment. *International Journal of Climatology*, **22**, 1441-1453.

- Koch, E., Bruns, E., Chmielewski, F.M., Defila, C., Lipa, W. and Menzel, A., 2009. Guidelines for plant phenological observations, 41 pp, WMO Technical Commission for Climatology, Open Program Area Group on Monitoring and Analysis of Climate Variability and Change (OPAG2). Available at: <http://www.omm.urv.cat/documentation.html> (accessed 2013-09-12)
- Körner C, Basler D (2010) Phenology Under Global Warming. *Science*, **327**, 1461-1462.
- Kramer K (1994) Selecting a Model to Predict the Onset of Growth of *Fagus sylvatica*. *Journal of Applied Ecology*, **31**, 172-181.
- Kramer K, Leinonen I, 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. *International Journal of Biometeorology*, **44**, 67-75.
- Langlet O (1960) Mellaneuropeiska granprovenienser i svenskt skogsbruk. In: *Kungliga Skogs- och Lantbruksakademiens Tidskrift*. pp Page, Stockholm, Statens skogsforskningsinstitut.
- Larcher W (2003) *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, Springer.
- Laube J, Sparks TH, Estrella N, Menzel A (2014) Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist*, **202**, 350-355.
- Liesebach M, Rau H-M, König AO (2010) Fichtenherkunftsversuch von 1962 und IUFRO-Fichtenherkunftsversuch von 1972. (ed Versuchsanstalt Badnf) pp Page, Göttingen.
- Lieth H (1974) Phenology and genecology of woody plants. In: *Phenology and seasonality modeling*. (ed Lieth H) Berlin, Springer-Verlag.
- Lim PO, Kim HJ, Nam HG (2007) Leaf Senescence. *Annual Review of Plant Biology*, **58**, 115-1136.
- Linderholm HW (2006) Growing season changes in the last century. *Agricultural and Forest Meteorology*, **137**, 1-14.
- Linkosalo T, Häkkinen R, Hänninen H (2006) Models of the spring phenology of boreal and temperate trees: is there something missing? *Tree Physiology*, **26**, 1165-1172.
- Linkosalo T, Lappalainen HK., Hari P (2008) A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree Physiology*, **28**, 1873-1873.
- Mátyás C, Ackzell L, Samuel CJA (2004) EUFORGEN Technical Guidelines for genetic conservation and use for Scots pine (*Pinus sylvestris*). pp Page, Rome, Italy, International Plant Genetic Resources Institute.
- Meier U (2001) Growth stages of mono- and dicotyledonous plants. In: *BBCH Monograph*. (ed Meier U) pp Page, Federal Biological Research Centre of Agriculture and Forestry.
- Menzel A (2003) Plant Phenological Anomalies in Germany and their Relation to Air Temperature and NAO. *Climatic Change*, **57**, 243-264.
- Menzel A, Estrella N, Heitland W, Susnik A, Schleip C, Dose V (2008) Bayesian analysis of the species-specific lengthening of the growing season in two European countries and the influence of an insect pest. *International Journal of Biometeorology*, **52**, 209-218.
- Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature (London)*, **397**, 659-659.

- Menzel A, Fabian P (2001) Climate change and the phenology of European trees and shrubs. In: *Impacts of Climate Change on Wildlife*. (eds Green R, Harley M, Spalding M, Zöcker C) Cambridge, RSPB.
- Menzel A, Sparks T (2006) Temperature and plant development, phenology and seasonality. In: *Plant Growth and Climate Change*. (eds Morison Jil, Morecroft Md) Oxford, Blackwell Publishing Ltd.
- Menzel A, Sparks TH, Estrella N, Roy DB (2006) Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography*, **15**, 498-504.
- Migliavacca M, Sonnentag O, Keenan TF, Cescatti A, O'Keefe J, Richardson AD (2012) On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences*, **9**, 2063-2083.
- Morecroft MD, Paterson JS (2006) Effects of temperature and precipitation changes on plant communities. In: *Plant Growth and Climate Change*. (eds Morison Jil, Morecroft Md) Blackwell Publishing Ltd.
- Morecroft MD, Stokes VJ, Morison JIL (2003) Seasonal changes in the photosynthetic capacity of canopy oak (*Quercus robur*) leaves: the impact of slow development on annual carbon uptake. *International Journal of Biometeorology*, **47**, 221-226.
- Morin X, Augspurger C, Chuine I (2007) PROCESS-BASED MODELING OF SPECIES' DISTRIBUTIONS: WHAT LIMITS TEMPERATE TREE SPECIES' RANGE BOUNDARIES? *Ecology*, **88**, 2280-2292.
- Myking T (1997) Effects of constant and fluctuating temperature on time to budburst in *Betula pubescens* and its relation to bud respiration. *Trees*, **12**, 107-112.
- Myking T, Heide OM (1995) Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiology*, **15**, 697-704.
- Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, **13**, 1860-1872.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.
- Partanen J (2004) Dependence of photoperiodic response of growth cessation on the stage of development in *Picea abies* and *Betula pendula* seedlings. *Forest Ecology and Management*, **188**, 137-148.
- Partanen J, Hänninen H, Häkkinen R (2005) Bud burst in Norway spruce (*Picea abies*): preliminary evidence for age-specific rest patterns. *Trees - Structure and Function*, **19**, 66-72.
- Partanen J, Koski V, Hänninen H (1998) Effects of photoperiod and temperature on the timing of budburst in Norway spruce (*Picea abies*). *Tree Physiology*, **18**, 811-816.
- Pau S, Wolkovich EM, Cook BI *et al.* (2011) Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, **17**, 3633-3643.
- Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531-544.
- Richardson AD, Anderson RS, Arain MA *et al.* (2012) Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. *Global Change Biology*, **18**, 566-584.

- Richardson AD, Black TA, Ciais P *et al.* (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society*, **365**, 3227-3246.
- Richardson AD, Keenan F, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, **169**, 156-173.
- Richardson AD, O'Keefe J (2009) Phenological Differences Between Understory and Overstory: A Case Study Using the Long-Term Harvard Forest Records. In: *Phenology of Ecosystem Processes*. (ed Noormets A) pp Page. New York, Springer.
- Richardson AD, Schenck Bailey A, Denny EG, Martin CW, O'Keefe J (2006) Phenology of a northern hardwood forest canopy. *Global Change Biology*, **12**, 1174-1188.
- Rohde A, Bastien C, Boerjan W (2011) Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiology*, **31**, 472-482.
- Schaber J, Badeck FW (2003) Physiology-based phenology models for forest tree species in Germany. *International Journal of Biometeorology*, **47**, 193-201.
- Skrøppa, T., 2003. EUFORGEN Technical Guidelines for genetic conservation and use for Norway spruce (*Picea abies*), 6 pp, International Plant Genetic Resources Institute, Rome, Italy.
- Smith B, Prentice Ic, Sykes M, T. (2001) Representation of Vegetation Dynamics in the Modelling of Terrestrial Ecosystems: Comparing Two Contrasting Approaches within European Climate Space. *Global Ecology and Biogeography*, **10**, 621-637.
- Søgaard G, Johansen Ø, Nilsen J, Junttila O (2008) Climatic control of bud burst in young seedlings of nine provenances of Norway spruce. *Tree Physiology*, **29**, 311-320.
- Sparks TH, Menzel A (2002) Observed changes in seasons: an overview. *International Journal of Climatology*, **22**, 1715-1725.
- Stöckli R, Vidale PI (2004) European plant phenology and climate as seen in a 20-year AVHRR land-surface parameter dataset. *International Journal of Remote Sensing*, **25**, 3303-3330.
- Ununger J, Ekberg I, Kang H (1988) Genetic control and age-related changes of juvenile growth characters in *Picea abies*. *Scandinavian Journal of Forest Research*, **3**, 55-66.
- Vakkari, P., 2009. EUFORGEN Technical Guidelines for genetic conservation and use of silver birch (*Betula pendula*), 6 pp, Biodiversity International, Rome, Italy.
- Vegis A (1964) Dormancy in higher plants. *Annual Review of Plant Physiology*, **15**, 158-224.
- Vitasse Y (2013) Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist*, **198**, 149-155.
- Vitasse Y, Basler D (2012) What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research*, **132**, 1-8.
- Vitasse Y, Basler D (2013) Is the use of cuttings a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? *Tree Physiology*, **34**, 174-183.
- Vitasse Y, Porté AJ, Kremer A, Michalet R, Delzon S (2009) Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia*, **161**, 187-198.

- Wallman P, Svensson MGE, Sverdrup H, Belyazid S (2005) ForSAFE—an integrated process-oriented forest model for long-term sustainability assessments. *Forest Ecology and Management*, **207**, 19-36.
- Westin J, Sundblad G Strand M, Hällgren JE (2000) Phenotypic differences between natural and selected populations of *Picea abies*. II. Apical mitotic activity and growth related parameters. *Scandinavian Journal of Forest Research*, **15**, 500-509.
- Wolkovich EM, Cook BI, Allen JM *et al.* (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature*, **485**, 494-497.

