Dissertationes Forestales 234

Modelling intra- and inter-annual growth dynamics of Scots pine in the whole-tree carbon framework

Pauliina Schiestl-Aalto

Department of Forest Sciences
Faculty of Agriculture and Forestry
University of Helsinki

Academic dissertation

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Author: Pauliina Schiestl-Aalto

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Thesis Supervisors:
Professor Annikki Mäkelä
Department of Forest Sciences, University of Helsinki, Finland

Dr. Harri Mäkinen
Natural Resources Institute, Finland

Dr. Liisa Kulmala
Department of Forest Sciences, University of Helsinki, Finland

Pre-examiners:
Dr. Sirkka Sutinen
Natural Resources Institute, Finland

Dr. Remko Duursma
University of Western Sydney, Australia

Opponent:
Assistant Professor Nicolas Delpierre
Laboratoire Ecologie Systématique et Evolution, Université Paris Sud, France

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Environmental factors have a dual effect on growth as they affect both the momentary growth rate (direct effect) and the rate of ontogenetic development (indirect effect). Photosynthesis on the other hand is the source of carbon that is needed for growth, respiration and other purposes. There are two opposite theories about the factor determining growth rate: 1) the availability of carbon for growth (source limitation) and 2) limitation that environmental factors cause on tissue ability to grow (sink limitation). Understanding the responses of the growth of tree organs (wood, needles, roots) to environmental and other factors is important to be able to understand the changes in tree growth and carbon balance in changing climatic conditions.

The purpose of this study was to define the effects of temperature on Scots pine growth at different temporal scales and to estimate the relative importances of the source and sink effects on growth. For that, a dynamic growth model CASSIA (Carbon Allocation Sink Source InterAction) was constructed.

CASSIA was able to predict daily primary and secondary wood and needle growth rate variation with indirect and direct effects of temperature. In addition, the temperature of warm previous late summer was observed to lead to enhanced length of the growth period (in temperature accumulation units) of shoots in the following year. Growth onset during spring was observed to be a continuous process determined by temperature accumulation, instead of momentary temperatures.

Short-term growth variations in normal conditions were concluded to be sink limited because CASSIA was able to predict the within year growth with temperature and without direct effect of photosynthesis or stored carbon. On the other hand carbon source effect (gross primary production) was needed to produce the between year variation in growth.
According to the results of this study, growth is limited by a complex combination of sink and source effects. Furthermore, environmental factors affect growth at different time scales varying from instantaneous effects to delayed effects from previous year(s). More research is needed to identify the factors determining the carbon flows to different processes.

Keywords: phenology, carbon balance, dynamic modelling, growth variation, sink-source dynamics

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LIST OF ORIGINAL ARTICLES

This thesis is based on the following three research articles, which are hereafter referred to in the text by their Roman numerals. The articles are reprinted with the kind permission of their publishers

I. Schiestl-Aalto P., Nikinmaa E., Mäkelä A. (2013) Duration of shoot elongation in Scots pine varies within crown and between years. Annals of Botany - London. 112(6):1181-1191. https://doi.org/10.1093/aob/mct180

II. Schiestl-Aalto P., Kulmala L., Mäkinen H., Nikinmaa E., Mäkelä A. (2015) CASSIA–a dynamic model for predicting intra-annual sink demand and interannual growth variation in Scots pine. New Phytologist 206(2):647-659. https://doi.org/10.1111/nph.13275

III. Schiestl-Aalto P., Mäkelä A. (2016) Temperature dependence of needle and shoot elongation before bud break in Scots pine. Tree Physiology 1-10 doi: https://doi.org/10.1093/treephys/tpw120

Author´s contribution:
Pauliina Schiestl-Aalto is responsible for the summary of the thesis. In paper **I** Pauliina Schiestl-Aalto was responsible for gathering part of the measurement data, the major part of the data analysis and calculations and writing the bulk of the article. In paper **II** Pauliina Schiestl-Aalto was responsible for the most of the modelling work. She conducted part of the measurements as well as data analysis and interpretation and participated in writing the article. In paper **III** Pauliina Schiestl-Aalto was responsible for measurements and data analysis and interpretation in addition to writing the bulk of the manuscript.

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INTRODUCTION

Background

Research on tree growth has been extensive and long-term. Woody growth can be divided into primary growth and secondary growth, which comprise the lengthening of shoots and the growth of a new annual ring, respectively. Woody growth has been of special interest from the point of view of production ecology (e.g. Huuskonen and Miina 2007). Previous studies have revealed a variety of effects of environmental and other factors on the growth of wood (e.g. Babst et al. 2013), leaves (e.g. Norgren and Elfving 1994) and roots (Valdés et al. 2006). For example, some important results of the temperature dependence of growth date back decades or even centuries (De Réaumur 1735, Sarvas 1972). Another intensively studied research field is the carbon exchange of forest stands and individual trees or tree organs. Carbon bound into living biomass and released from living biomass determine the carbon balance of the forest trees (Kolari et al. 2009). This study combines the growth processes of individual tree organs and analyses them from the point of view of whole-tree carbon balance.

Environmental conditions and carbon availability as alternative factors that determine growth timing and intensity are under intense debate (e.g. Körner et al. 2015). The main objective of this study was to assess the effects of both fluctuating weather and carbon source on the growth of Scots pine (*Pinus sylvetrsis* L.) organs on different temporal scales. An understanding of the functionality of a whole tree that consists of individual, divergent organs with different responses to environmental and other factors is needed to be able to predict the changes in tree growth and carbon balance that occur under changing climate conditions.

Phenology

Plants in the boreal zone have a clear annual rhythm. The dormancy period in winter is followed by the onset of development and growth in spring. Growth, reproduction and largely photosynthesis occur during the active period, and these functions fall into dormancy in the autumn (Fig. 1). Leith (1974) defines: "*Phenology is the study of the timing of recurrent 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.*" Timing of individual phenological events such as bud burst have been studied widely and for a long time (Linkosalo et al. 2008). Phenological events can be momentary such as bud burst or the opening of catkins (Sarvas 1972) or it can be continuous such as growth.

Nowadays phenology has regained increasing interest because climate change will alter the driving factors of phenological events and thus the progression of the annual cycle (Linkosalo et al. 2000, Caffarra and Donnelly 2011). The timing of growth onset has been shown to be strongly temperature determined, thus it has been predicted and already observed to occur earlier in the year (Menzel and Fabian 1999, Peñuelas et al. 2002, Linkosalo et al. 2009). The magnitude of this shift and changes for other phenological events are, however, difficult to predict because the joint effects of environmental factors on the progress of the annual cycle are poorly known. We must understand the real mechanisms by which

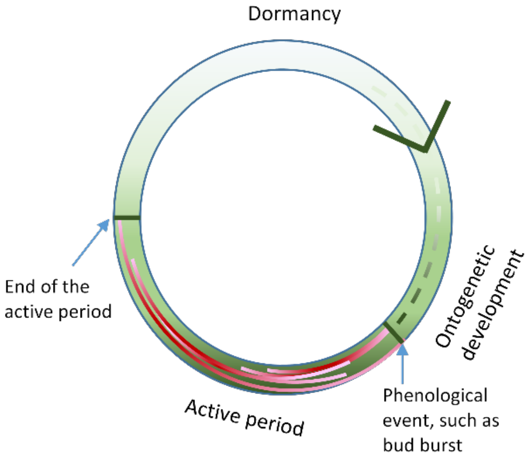

Figure 1. The annual cycle. Ontogenetic development takes place throughout the year, even before visible growth reactions. The red lines in the active period represent the growth periods of different organs or active periods of processes the length of which differs from the whole active period. The green colour depicts the activity of growth and other processes in the tree.

environmental factors affect phenology to be able to predict how trees (different species, different tree organs) react to the changing environment.

Temperature is the most important driving factor of phenology in the boreal zone (Hari 1972, Sarvas 1972, Chuine et al. 2010). De Réaumur (1735) observed that plants respond to temperatures above a certain threshold value for their development to ensue and he used this phenomenon as the basis for creating the temperature sum model (eq. 1), which remains the most used means of quantifying the effect of temperature on growth. Temperature sum is calculated as:

$$T_n^S = \sum_{i=t_0}^{n} \Delta_i\,, \quad \text{where} \quad \Delta_i = \begin{cases} T_i - T_{th}, & T_i \geq T_{th} \\ 0, & T_i < T_{th} \end{cases} \tag{1}$$

where T_i is the temperature at day or hour i, t_0 is the starting time of temperature sum accumulation (for example the beginning of year or the vernal equinox) and T_{th} is a threshold temperature parameter. Temperature is also the key factor for spring recovery of photosynthesis in the boreal zone (Suni et al. 2003), although Böttcher et al. (2014) observed that the timing of photosynthetic recovery has a stronger correlation with the timing of snow melt than with air temperature alone. However, snow melt is also controlled by temperature.

In addition to temperature, e.g. light as measured by either day or night length (Koski and Sievänen 1985, Caffarra and Donnelly 2011) and water availability (Peñuelas et al. 2002, Laube et al. 2014) have been shown to affect the timing of phenological events.

More generally, the concept of “ontogenetic stage of development” is one way to describe the occurrence of phenological events and processes. The stage of development describes the position of the observation object (e.g. a tree) within the annual cycle (Fig. 1). Temperature and other environmental factors are the driving factors for the progression of stage of development, s. The calculation is initiated at either the beginning of the year or e.g. at vernal equinox, after which stage of development proceeds as:

$$\frac{\mathrm{d}s}{\mathrm{d}t} = r(E(t)) \tag{2}$$

where r is the rate of the progress of the stage of development that depends on environmental factors ($E(t)$). For example, with the temperature sum model $r(E(t)) \propto \Delta_i$ (eqs 1 and 2). A comprehensive introduction to the different models of ontogenetic stage of development is available in Hari and Häkkinen (1991) and Hänninen and Kramer (2007). These models have been used in various fields of phenological studies such as spring phenology and bud break, shoot growth, leafing-out and autumn dormancy (Chuine et al. 2006, Linkosalo et al. 2008, Polgar et al. 2011).

Dependence of growth on phenology and environmental factors

Growth occurs during the active period of the annual cycle. However, the growth period does not necessarily last for the whole active period and growth can cease significantly earlier than e.g. the photosynthetically active period (Fig. 1). The timing and the rates of growth of different parts of a tree in relation to each other can also differ under different environmental conditions. An individual active period, “growing season” can be defined for each organ.

The effect of environmental factors (especially temperature) on growth is twofold. First, environmental factors drive phenology i.e. the stage of development and thus both the onset of the growth period and, in some cases, the duration of the growth period. This is the indirect effect of environmental factors on growth. Second, environmental factors have a direct

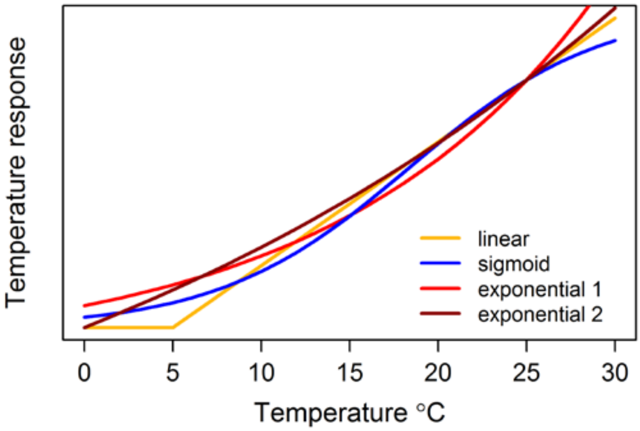

Figure 2. Linear, exponential 1 (light red), as suggested for maturation by Hari et al. (1977), exponential 2 (dark red), as suggested for growth by Kanninen et al. (1982), and sigmoid (Sarvas 1972) temperature response curves of maturation and growth.

(instantaneous) effect on growth. Growth rate has been assumed to depend linearly (eq. 1), exponentially (Hari et al. 1977) or sigmoidially (Sarvas 1974, Hänninen 1990, Kramer 1994) on temperature with a time lag of a few hours (Hari et al. 1977). The responses are similar when temperature values are above 10°C, whereas the differences at low temperatures are large (Fig. 2).

Growth typically occurs in such a way that growth is slow at the beginning and at the end of the growing period, whereas in the middle of the period, growth is fast. For example shoot growth has been noted to follow a sine-shaped growth pattern when temperature is constant (Oleksyn et al. 2001, Chuine et al. 2006). The daily variation of environmental factors induces variation to this sine-shaped rhythm (Fig. 3).

Scots pine shoots have been observed to follow a predetermined growth habit, which suggests that the final length of yearly shoot growth depends on the environmental factors of the preceding year, when the bud that contains all the needle fascicles is formed (Mäkinen 1998, Salminen and Jalkanen 2005). At high latitudes, the length of the growth period of a Scots pine shoot in temperature sum units is rather constant (Salminen and Jalkanen 2007). Thus, the length of the growth period in time units depends on temperature in such a way, that at high temperature growth ceases earlier than at low temperature. The momentary growth rate increases with temperature, therefore the final length of a shoot does not depend much on the temperature during the elongation period.

New xylem is formed as cells of the cambium divide into xylem mother cells, which further divide into xylem daughter cells (Plomion et al. 2001). Development of the daughter cells includes the phases of cell expansion and growth of secondary wall before maturity. The division and cell expansion determine diameter growth, whereas growth of secondary wall determines biomass growth (Antonova and Stasova 1993).

The environmental factors and their combinations that affect growth directly or indirectly are species- and organ-specific. For example, contrary to shoot growth ring width is mostly affected by the environmental factors of the current growing season (Korpela et al. 2011, Babst et al. 2013). The inference of this phenomenon is that the length of this secondary

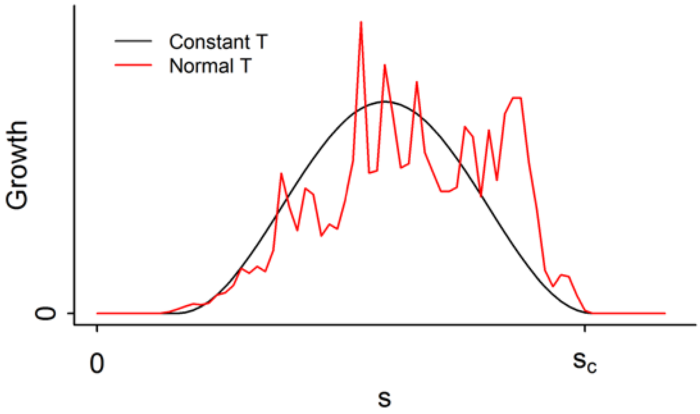

Figure 3. Modelled daily shoot growth in relation to stage of development (s) with constant temperature (black) and measured (varying) temperature (red, temperature is measured at SMEARII station in 2003).

growth period of Scots pine in temperature sum units increases with more favourable environmental conditions. More generally this can be expressed as the stage of development units in which also other environmental factors can also be accounted for. Thus, the effect of phenology on secondary growth is divergent from that of shoots. Further, in contrast to Scots pine, the cessation of silver birch (*Betula pendula* Roth) shoot growth has been observed to depend on the combination of temperature sum and night length (Koski and Sievänen 1985).

Usually momentary growth is understood to depend on air temperature, but it is noteworthy that growth actually is affected by meristem temperature rather than air temperature (James et al. 1994). Correspondingly, Gričar et al. (2007) observed that the rate of cell division increased in the cambium of a heated stem and decreased in a cooled stem compared to controls.

Besides temperature, the availability of water is globally a significant factor that affects growth (Mina et al. 2016). In the northern humid climate, temperature has been the most important factor that restricts growth. However, if summer precipitation does not significantly increase simultaneously with higher temperature (IPCC 2013), enhanced transpiration induces more frequent and intensive drought periods. Drought affects growth indirectly via reduced photosynthetic production due to reduced stomatal opening and thus reduced carbon assimilation and also non-stomatal factors such as lower carboxylation capacity (Lansberg and Waring 1997, Zhou et al. 2013). Water availability has also a direct effect especially on secondary growth via turgor pressure, which drives cell enlargement (Hölttä et al. 2010, Nikinmaa et al. 2014) and via cambial activity, which is decreased under drought conditions (Deslauriers et al. 2016). Low levels of soil moisture also decrease or inhibit root growth (Bowen 1970, Valdés et al. 2006).

Carbon balance of a tree

Carbon balance of a tree consists of the following processes: consists of (1) carbon gain in photosynthesis, (2) carbon release due to energy expenditure on vital functions or growth (respiration), senescence of foliage, branches and roots, as well as for example seed production, volatile organic compound (VOC) synthesis and root exudates and (3) bound carbon that can be divided into structural carbon (growth) and non-structural carbon storage (NSC) that can be used for balancing the short-term differences between carbon assimilation and consumption (Fig. 4). The rate of photosynthesis is affected by the amount of photosynthetically active radiation, the temperature, carbon dioxide level and water availability (moisture in the root zone in addition to the atmosphere vapour pressure deficit) (Mäkelä et al. 2008). As noted above, growth is species- and organ specifically affected by a variety of environmental factors at different temporal scales. Growth respiration is proportional to the rate of growth and thus its timing is concurrent with the timing of growth (Penning de Vries 1974). In contrast, metabolism and therefore maintenance respiration are active throughout the year. Plant metabolism is highly temperature dependent, which leads to a strong short-term correlation between maintenance respiration and air temperature (Kolari et al. 2009). The rate of maintenance respiration is thus significantly lower but nevertheless positive during winter. Hence, the enhancing and restricting environmental factors of photosynthesis and carbon consuming processes are not the same and the carbon gain in photosynthesis and carbon loss in consumption differ with respect to timing or rate.

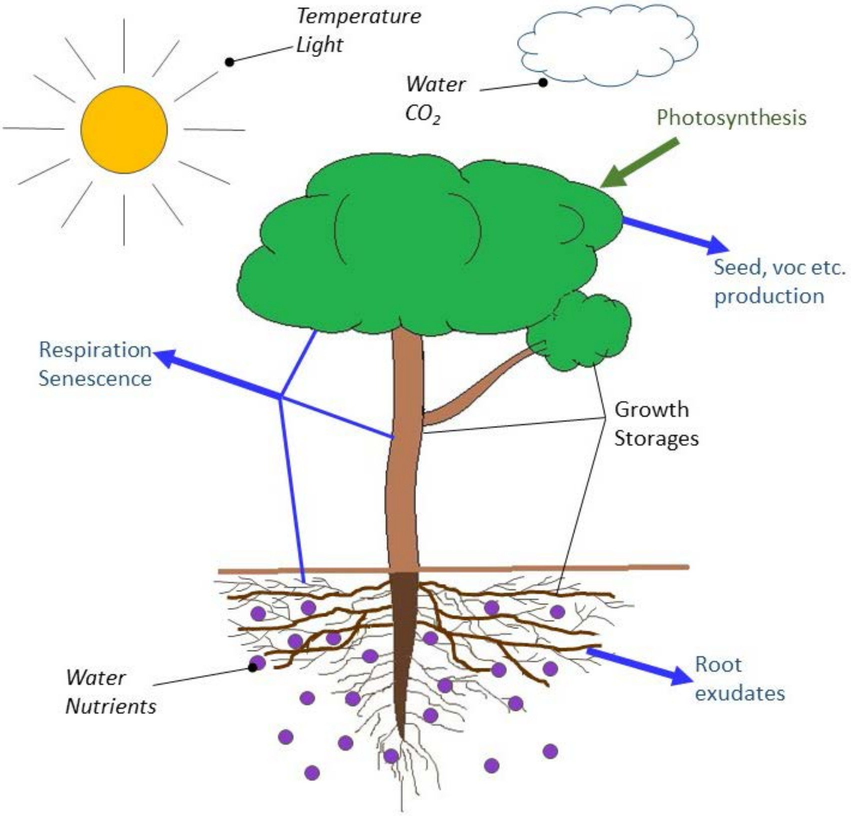

Figure 4. Components of carbon balance of a tree. Carbon gain (green arrow) and loss (blue arrows) and environmental factors (in Italics).

Although over short timescales carbon assimilation and consumption as well as growth of different tree organs may be decoupled, maintaining on one hand a balance between resources and use and on the other hand a functional balance between tree organs is important for tree survival and optimal development. The idea of the “pipe model”, was originally introduced by Shinozaki et al. (1964a,b) and later used and specified by a multitude of researchers (e.g. Mäkelä and Valentine 2006, Schneider et al. 2011, Gehring et al. 2015). The pipe model suggests a constant (site-, species- etc. specific) ratio between leaves, sapwood and roots. Correspondingly, the ratio between respiration and photosynthesis is found to be nearly constant on longer timescales (Gifford 2003). Thus, over a medium time scale (years) the carbon fluxes or growth of different organs have to be related to each other and therefore, there have to be mechanisms that allow the tree to maintain a balance between these components.

In addition to the above-discussed environmental factors, nutrient availability especially that of nitrogen have a great effect on carbon balance (Ryan 2013). Nitrogen enhances both photosynthesis (Roberntz 2001) and growth (Sigurdsson et al. 2013) and is one of the most limiting long-scale factors for growth in the boreal zone (Tamm 1991). Optimal nitrogen treatment may increase growth many-fold compared to controls (Bergh et al. 1999). However, the nitrogen availability is a rather stable variable and thus it does not cause any short term changes in the carbon balance.

Sink and source theories

A carbon source by definition produces carbon in the phloem and a carbon sink carbon from the phloem (Clifford 1992, Lacointe 2000). The flux of carbon from source to sink is determined by relative source strength and sink strength and their spatial distance (Sievänen et al. 2000). Source limitation theory assumes that tree growth is limited by carbon availability and thus the photosynthetic efficiency determines the rate of growth (Wiley and Helliker 2012). All carbon produced by photosynthesis is actively used for carbon limited processes. The ratio of gross primary production (GPP) to (aboveground) growth has been reported to be nearly constant across site types and age classes in boreal forests (Zha et al. 2013). An implication of this finding is that most of the terrestrial biosphere models and the dynamic global vegetation models are based on source limitation theory (see Leuzinger et al. 2013, Guillemot et al. 2015).

Sink limitation theory is based on the assumption that carbon use for growth and other purposes is limited by sink strength which describes the ability of a sink to pull carbon from the phloem (Marcelis 1996). Sink strength is a combination of the capacity and activity of the sink (Clifford 1992), which are determined by environmental factors and the inherent state of the plant. Photosynthesis and/or NSC storages are sufficient to cover the demand created by the sinks. The significance of storage as a carbon buffer is emphasized in sink limitation theory (Hoch and Körner 2012). Thus, carbon availability does not limit growth in any situation but growth is limited by shortage of warmth, moisture or nutrients (Körner 2015).

The observation that photosynthesis is still active at significantly lower temperatures than temperatures required for growth is used as evidence that supports the sink limitation theory (Palacio et al. 2014). Delpierre et al. (2016b) observed a growth decrease with high vapour pressure deficit (VPD) even though GPP was not decreased. NSC storages are reported to increase or to stay at the same level with increasing elevation (decreasing temperature), which is assumed to be a consequence of growth limitation by temperature and thus carbon surplus (Piper et al. 2006, Hoch and Körner 2012, Simard et al. 2013). Petit et al. (2011) observed that heating of Norway spruce (*Picea abies* (L.) Karst.) buds enhanced the shoot length growth at high altitudes but not at low altitudes, which was interpreted as a temperature limitation at the colder high altitude site. Increased nutrition has been shown to have a strong positive effect on growth (e.g. Susiluoto et al. 2010). Furthermore, photosynthesis has been shown to increase with increasing CO_2 levels and temperature (Uddling and Wallin 2012, Wallin et al. 2013). In spite of increased photosynthesis additional nitrogen is needed to achieve a positive response of growth for elevated CO_2 and temperature levels (Sigurdsson et al. 2013). Leuzinger et al. (2013) succeeded in improving the biomass estimation of a dynamic global vegetation model by estimating tree growth with a sink-limited instead of source-limited model. These results suggest growth limitation that is not regulated by carbon deficiency.

The same environmental factors, which according to the sink-limitation theory are assumed to limit growth (or other consumption) directly also limit photosynthesis (Guillemot et al. 2015). Therefore, separating the effects of source and sink strength is not straightforward. Most of the evidence used for supporting either one of the limitation theories is equivocal and can also be countered by contradictory interpretations. Wiley and Helliker (2012) proposed that large storage by high elevation trees are not necessarily a sign of carbon surplus but rather a survival strategy for preventing carbon starvation. Therefore, increasing NSC storage could alternatively indicate a scarcity of carbon for growth. Several studies propose a combined effect of sink and source limitations or find no clear signs supporting only one of the two hypotheses (e.g. Gruber et al. 2011, Guillemot et al. 2015, Takahashi and Furuhata 2016).

Combining phenology and carbon flows

As stated above, the amount of carbon used for the growth of a tree (per day or per year) is defined by either the amount of photosynthetised carbon or the growth sink strenght. Allocation patterns determine how assimilated carbon is distributed amongst the tree organs. According to Lacointe (2000) carbon partitioning has been defined by the following approaches: (1) constant allocation parameters, (2) the maintenance of optimal tree structure, (3) transport-resistance models or (4) defining the relative sink strengths of tree organs. The assumptions that underlie these approaches vary. The applicability of any one of these methods in carbon allocation modelling is, however, questionable in a changing environment (Franklin et al. 2012, Mäkelä 2012).

On short timescales (days) it seems that growth of at least some tree organs of some tree species can be adequately described with the effect of temperature only (Hari et al. 1970). There are also between-year delays in environmental factors that affect growth such as bud development and shoot growth (Salminen and Jalkanen 2007). In addition, we know that a sink and source must be balanced over a longer time scale (years) in such a way that the carbon storages neither become depleted nor increase infinitely and that there remains a functional balance between tree organs (Mäkelä and Valentine 2006). Therefore, we can assume that a description of a combination of allocation patterns is needed. We must be able to describe the direct and indirect effects of environmental factors both on growth and photosynthetic production and determine which one of these limits growth over different temporal scales to be able to predict how the timing and amount of carbon production and usage respond to changes in environmental factors. Especially if stress conditions, such as drought, become more prevalent and severe the relative importance between the sink and source limitations as growth limiting factors may change.

A further question remains as to how the timings of the growth periods of different organs will change. As growth onset occurs earlier, the risk of spring frost damage may increase in spite of the higher mean temperatures (Linkosalo et al. 2000). Moreover, the timing of growth cessation is determined by different factors than growth onset and thus the change in the length of the growth period is not easy to predict (Way 2011). Under current conditions growth of most of the tree organs does not occur throughout the entire growing season (e.g. Hari et al. 1970, Huang et al. 2014). The mechanisms by which the lengthened period of favourable environmental conditions can or cannot be utilized is therefore of great significance to the carbon balance of the boreal forests.

Objectives

The aim of this study was 1) to assess the influence of temperature on the growth of Scots pine and 2) to gain insights into the interaction between the carbon consumption for the different growth events and the whole tree carbon balance. The main tasks were:

- Quantifying the effect of temperature on the timing of growth onset, and growth cessation and on the rate of growth during the growth period (**I-III**)
- Investigating the interrelations of the growth dynamics of different tree organs (**II, III**)
- Estimating the importance of carbon source and sink effects on growth timing and rate and on the carbon balance of a tree (**II**)

MATERIALS AND METHODS

Study sites

The measurements were conducted at SMEAR II station (Hari and Kulmala 2005), which is a Scots pine stand that was sown in 1962. The site is located in boreal zone, southern Finland (61.52 N, 24.17 E), it is medium fertile, and is classified as *Vaccinium* forest site type (Cajander 1926). The dominant tree height was reported as 14.5 m in 2001 and the basal area 24.3 m^2 ha^{-1} before and 17.9 m^2 ha^{-1} after thinning in 2002. The mean annual temperature is +3.5 °C and rainfall is 711 mm (calculated for the 1980-2009 period, Pirinen et al. 2012). The monthly mean temperatures vary from -7.7 °C (February) to 16.0 °C (July).

In order to study the detailed growth dynamics of shoots and needles**,** measurements were conducted nearby SMEAR II –station at Scots pine sapling stands 1 (**I** and **III**) and 2 (**III**), with 1400 and 2600 trees ha^{-1}, respectively. The mean ages of the stands were 6 years (*Sapling 1,* **I**) and 11 years (*Saplings 1* and *2,* **III**) and mean heights 2.0 m (*Sapling 1,* **I**), 5.0 m (*Sapling 1,* **III**) and 3.6 m (*Sapling 2,* **III**) at the beginning of the study periods.

Measurements

Environmental factors

Mean daily air temperature (T_a, °C) and total daily precipitation (mm) were calculated from values measured every minute at the height of 16.8 m. Soil water content (m^3 m^{-3}) was measured by time domain reflectometry (Ilvesniemi et al. 2010) and soil temperature (°C) of the B horizon (5-23 cm below the soil surface) at 15 minute time resolution.

NEE, GPP and respiration

Net ecosystem exchange of carbon (NEE, μmol m^{-2} s^{-1}) was measured by the closed-path eddy-covariance method at one minute intervals after which it was decoupled to gross primary production (GPP) and total ecosystem respiration (TER, μmol m^{-2} s^{-1}). The dependency of TER on soil temperature was derived from night time NEE measurements. Day-time NEE was partitioned into GPP and TER using the obtained temperature dependency. Instrument documentation is described by Vesala et al. (2005) and data processing by Kolari et al. (2009).

Growth

The length growth of new shoots and needles was measured by digital caliper or later with a ruler (for shoots) in order to determine the within-year dynamics of growth and short-term responses of growth to environmental factors (**I, II, III,** Table 1).

Table 1. Details of the measurements taken for studies I, II and III.

	I	**II**	**III**
Years	2002-2009	1997-2012	2012, 2014-2015
Study period	Growing season	Growing season	March-June
Study sites	SMEAR II, Sapling 1	SMEAR II	Saplings 1 and 2
Temperature, ºC	x	x	x
GPP µmol m^{-2} s^{-1},		x	
Soil water content, m^3m^{-3}		x	
Shoot length, mm	x	x (2002-2012)	x
Needle length, mm		x (2003-2012)	x
Xylogenesis, nr cells		x	
Nr of shoots or needles / sampling date	13-34	13-33	5

For measuring the number of cells in each phase of xylem formation, microcore samples were taken 1-2 times/week from four trees during growing seasons of the 2007-2010 period. For a detailed description of the method and laboratory analyses see Kalliokoski et al. (2012) and Jyske et al. (2014).

The yearly stem elongation of seven trees and the radial increment of 14 trees were measured and used for studying the between-year variation in growth. The measurements cover years 1997-2012 for stem elongation and 1997-2011 for radial increment (**II**).

Model

Basis

A model called CASSIA (Carbon Allocation Sink Source InterAction, **II**) was developed for examining which environmental or inherent factors affect the carbon balance of a tree at different timescales. The model was used especially to determine which one is the main driving mechanism for carbon allocation, source or sink. The model consists of different pools and fluxes of carbon in a tree. It calculates with a daily time step the amount of carbon that is released through respiration, bound to growing tissues or stored as nonstructural carbon using air and soil temperature, soil moisture and photosynthesis (Fig. 5). A lighter version of the model was used to determine the daily growth rates for shoots (**I**) and for needles (**III**) without the whole tree carbon balance.

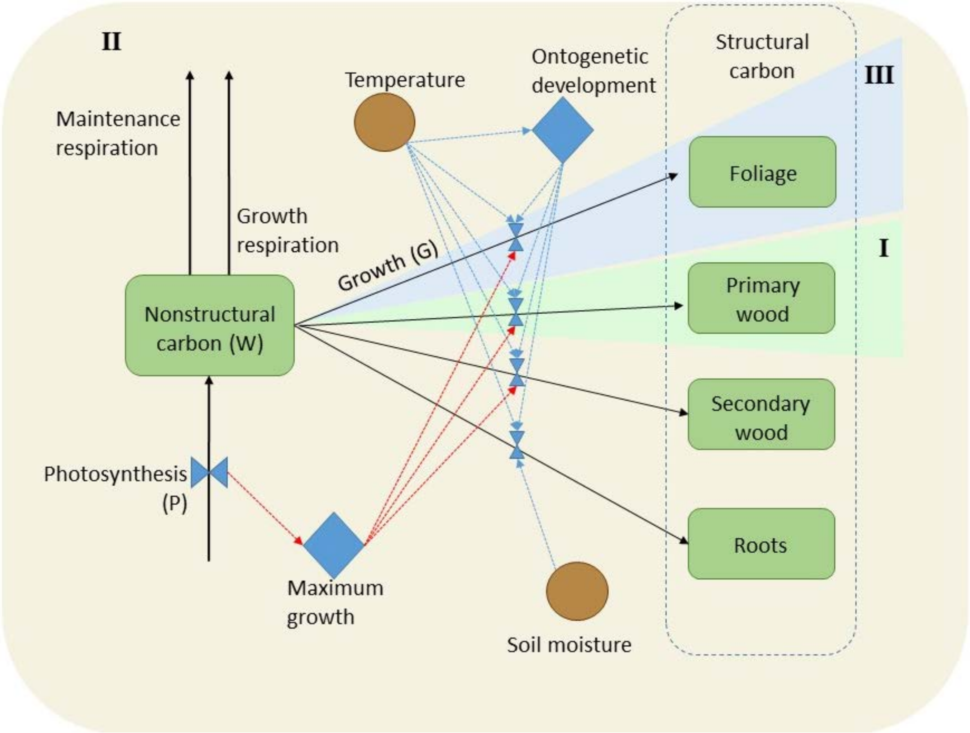

Figure 5. Model structure. State variables are shown in green rectangles and carbon flows are depicted by black arrows. Environmental factors are depicted by brown circles and inherent variables by blue diamonds. The red and blue arrows indicate source and sink effect, respectively. Coloured areas with roman numbers refer to contents studied in papers **I**, **II** and **III**.

Phenology and momentary growth

Modelling the phenology (stage of development, eq. 2) and the short term temperature response of organ growth were based on a growth model introduced by Pietarinen et al. (1982). Following the method described by Sarvas (1972), the dependence of growth and progress of the stage of development on temperature was given by:

$$\frac{\mathrm{d}s}{\mathrm{d}t} = g(t) = \begin{cases} 0, & T_a(t) < 0 \\ \frac{1}{1+e^{-\alpha(T-\beta)}}, & T_a(t) \geq 0 \end{cases} \qquad (3)$$

where $g(t)\epsilon[0{,}1]$.

The dependence of growth on phenology, $(f_i \epsilon[0{,}1])$, was described with a sine function (Fig. 3) or an asymmetric function depending on organ such that $f_i > 0\ when\ 0 < s_i < s_i^c$, where *i* is *N*, *S*, *D*, *R* for needles, primary wood, secondary wood and roots, respectively and s_i^c is the parameter that determines growth cessation in stage of development units. In the beginning of the year, $s_i(t = 0) = s_i^0 \leq 0$. Thus growth begins when the stage of development (s) has accumulated from s_i^0 to 0.

Dimensional growth (mm, $i = N, S$), the number of new cells (nr, $i = D$) and mass growth of roots (kg C, $i = R$) was calculated as:

$$\frac{\mathrm{d}x_i(t)}{\mathrm{d}t} = g(t) f_i\big(s_i(t)\big) L_i \tag{4}$$

where L_i is a maximum growth parameter ($i = N, S$: mm day^{-1}, $i = D$: nr of cells day^{-1}, $i = R$: kg C day^{-1}) which depends on GPP of the previous ($i = N, S$) or the ongoing ($i = D$) year. For roots L was assumed to be constant. Maximum growth was then reduced by suboptimal temperature or the effect of phenology.

*Combining growth functions with carbon flows (**II**)*

Carbon that was used for growth of needles was calculated as a constant amount of carbon per needle length unit. The number of new needles was assumed to depend on the environmental conditions during the period of bud formation (previous July-August). The carbon consumption for primary growth was calculated as a function of shoot length growth and initial basal area with a form factor and a density parameter.

In xylogenesis modelling, the new tracheids that are formed go through the phases of cell enlargement and cell wall thickening and end in maturity. Xylogenesis of one tracheid row was modelled and then generalized for the whole tree by using the mean tracheid size. Carbon is used for maintaining turgor pressure that is needed for cell enlargement and for cell wall thickening as a constant amount of carbon on each day that the tracheid stays in the cell formation phase. The carbon used for cell enlargement is released after the tracheid has reached its final size. The duration of the phases were assumed to be constant.

The above described step of the dimensional growth model is sink-based i.e. source does not limit growth. The "potential growth rate" ($G_{POT}(t)$) is thereafter reduced by the term $k(t)$ ($\epsilon[0,1]$) when the carbon source (stored carbon) falls below a critical level. Thus, the actualized growth, G, is:

$$G(t) = k(t) G_{POT}(t) \tag{5}$$

The change in the carbon storage was calculated as:

$$\frac{dW}{dt} = P(t) - R^M(t) - G(t) - R^G(t) \tag{6}$$

where $P(t)$ is photosynthesis (measured as GPP), $R^M(t)$ maintenance respiration and $R^G(t)$ growth respiration. Growth respiration was assumed to be proportional to growth with organ-specific parameters (Penning deVries 1974). Maintenance respiration was calculated for each fraction i with the biomass of the fraction and temperature as explanatory factors.

Use of the measurement data

Model parametrization

The parameters L_s, s_S^c and H_{s0} used in the shoot growth study were estimated first for the mean shoot length growth of each year as the mean length of all the shoots on each measurement day, and second for each shoot separately.

The parameters of the primary growth model in CASSIA (**II)** were estimated using the data for the year 2008 and parameters of secondary and needle growth model with the data obtained for the year 2009. The years were chosen according to the coverage of the measurement data. The parameters were estimated using the assumption that there is no short-term source limitation in growth (i.e., $k = 1$, eq. 5). Parameters L_i ($i = N, S, D$) were estimated using GPP values of either current ($i = D$) or previous ($i = N, S$) summer to evaluate the limiting effect of source at a longer time-scale.

In the needle growth study, the needle length model was revised and parameters $L_{N,}$ s_N^0 and s_N^c were estimated for the study years separately.

The parameter estimation was done by using the Excel Solver-tool (GRG Nonlinear solving method in SOLVER analysis tool; Microsoft Corporation, Redmond WA, USA) by minimizing the sum of squared residuals between the measured and predicted values.

Statistical analyses

The goodness of fit used in the shoot growth model (**I**) was evaluated by calculating the degree of determination (R^2), the root mean square error (RMSE) and bias for the length (total accumulated length on each measurement day) and growth of the shoot. Regression models were used for studying:

1) The relationship between the value of stage of development at growth cessation (s_S^c) and the value of maximum growth rate L_s and
2) The relationship between s_S^c and the temperature during bud formation (July–August period of the preceding year)

The calculations were carried out with R (lmer routine, R Development Core Team, 2013). P-values, deviance and Akaike´s Information Criteria (AIC) were used for evaluation and comparisons of the regressions.

A linear mixed model was formed between the needle and shoot length growth during the early growing season for the needle growth model (**III**). Further, two types of methods were used to evaluate the lower threshold of temperature for development progression during spring time. First, a method introduced by Rossi et al. (2007) was used whereby the timing of growth onset is assumed to follow momentary temperatures. Second, following Sutinen et al. (2012) temperature sum accumulation was compared to early growth of needles with various combinations of beginning dates, time steps and threshold temperatures of the temperature sum calculation. The analyses were carried out using R (R Development Core Team, 2015).

RESULTS

The effect of temperature on the timing and rate of growth

The timing of growth onset depended on temperature and specifically on temperature accumulation (defined e.g. as temperature sum or stage of development) rather than momentary temperatures (**III**). Growth onset was predicted to a satisfying level of accuracy for different years with a constant parameter of stage of development (**II**).

Growth cessation of shoots similarly followed temperature accumulation. However, growth cessation in temperature accumulation (stage of development) units was correlated with the temperature of the July – August period of the preceding year, which is the time when the new buds that are to grow in the following year are formed (**I**). If the preceding summer was warm the shoots grew for a longer period in the following year than they would if there had been a cold time of bud formation (Fig. 6).

Furthermore, temperature has a direct (instantaneous) effect on growth rate during the growing season. The model succeeded in explaining the daily growth variations with the direct effect of temperature and stage of development (as depicted in Fig. 3, **I**, **II**). The short-term temperature dependence was especially evident in shoot and needle growth due to more frequent measurement intervals compared with secondary growth. Growth was slow at the beginning and also at the end of the growth period but fast during the middle (phenology). However, the growth curve was uneven rather than smooth due to the day-to-day fluctuations of the direct temperature effect (Fig. 3).

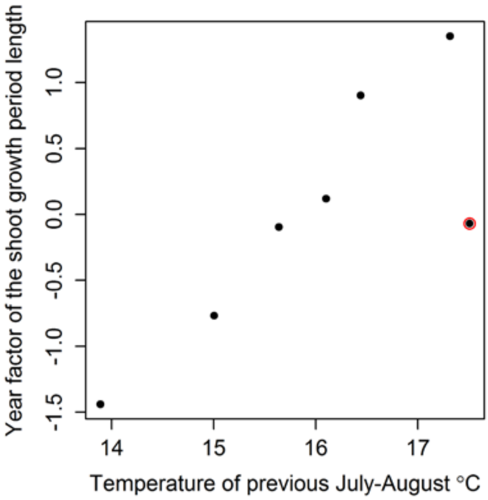

Figure 6. Temperatures during the bud formation period of July-August period of the preceding year and the values of a year effect in a regression between the length of the growth period and shoot length (regression 1 in I). The outlier year (demarked with a red circle) is the year 2007 that followed a severe drought period in July-August 2006 that had probably hindered bud formation.

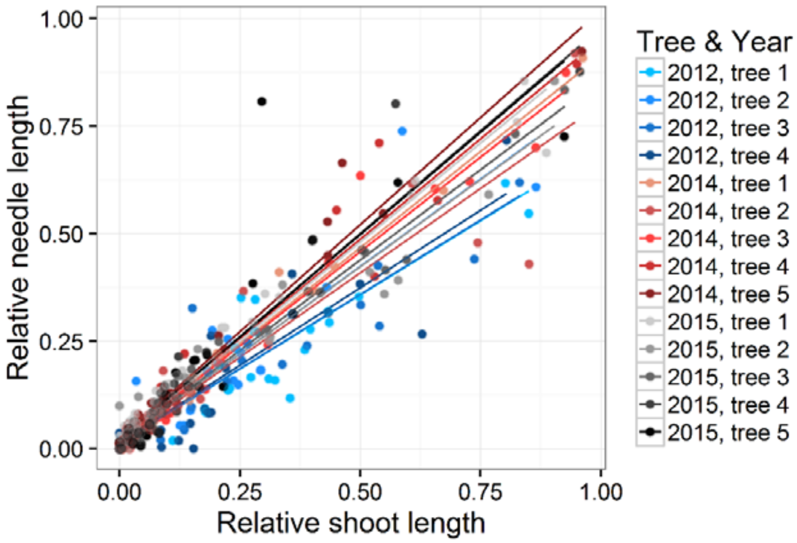

Figure 7. The relationship between the relative length of shoots and needles during the early growth period and the regression lines produced in a linear mixed model.

Interrelations of the growth dynamics of different tree organs

Originally needle growth had been defined to begin after shoot growth onset (**II**). However, in the detailed study of the early growth period, needle and shoot growth onset were observed to occur almost simultaneously (**III**, Fig. 7).

The relative progress of shoot growth was more rapid after onset compared to that of needle growth because the growth period of shoots was shorter than that of needles (Fig. 8). Secondary growth onset (new tracheids in the enlargement zone) occurred after the onset of needle and shoot growth and the secondary growth continued until September when all cells had finalized cell wall formation and become mature cells) (**II**). Root growth is slow in the spring because of low soil temperatures and lasts until late autumn if moisture condition is favourable.

Source and sink effects on growth timing and intensity and on the carbon balance of a tree

The amount of assimilated carbon was 24% higher in the year with the highest GPP (2013) than with the lowest GPP (1999). Photosynthesis was higher than the total carbon consumption in 10 out of 16 years. On average 48% (42–55%) of the photosynthesis production was released by maintenance respiration and 12% (11–14%) for growth respiration. Roots and secondary wood were the organs with largest carbon consumption for growth (Fig. 9)

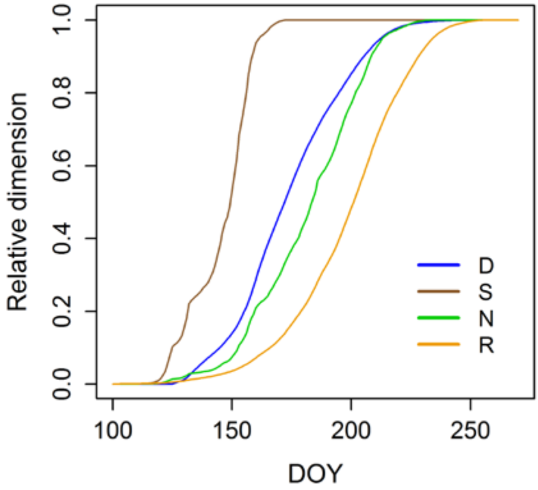

Figure 8. Timing of the growth periods of secondary wood (D), primary wood (S), needles (N) and roots (R) according to model results for the days of the year of 2008. Needle growth rhythm is modelled as a sine function (see **III**) and other tree parts as in **II**. DOY stands for day of the year.

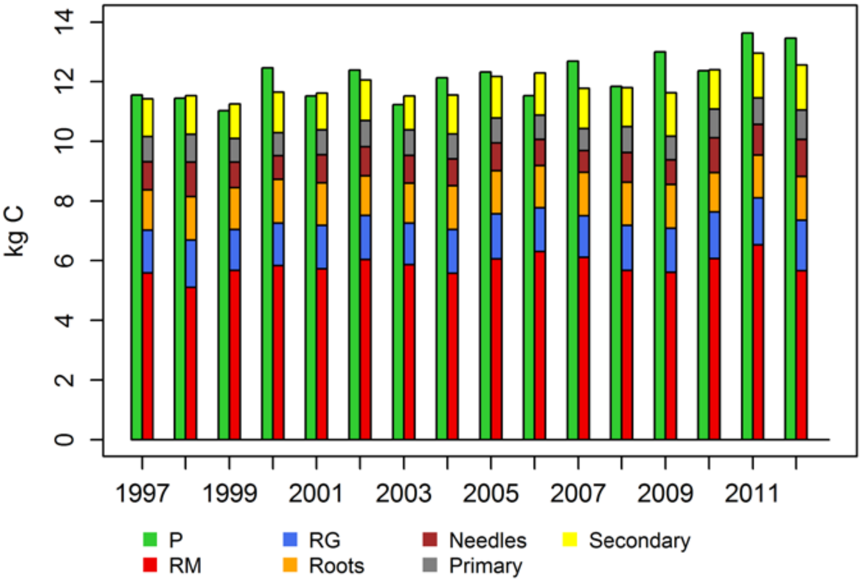

Figure 9. The components of carbon balance (**II**). Photosynthesis (P) is a source of carbon whereas RM (maintenance respiration), RG (growth respiration) and the growing organs are carbon sinks.

The model was able to predict within-year growth by modelling sink strength without source limitation (**I** and **II** with the assumption that storage parameter $k = 1$), thus it seems that the intra-annual variations in growth timing and intensity were caused by the sink effect (Figs 10, 11). On the other hand, a source effect (mainly parameter L_i, eq. 4) was needed for inducing the observed between-year variations of needle, primary and secondary growth (**II**, Fig. 12). These results indicate a combination effect of sink and source limitations on growth.

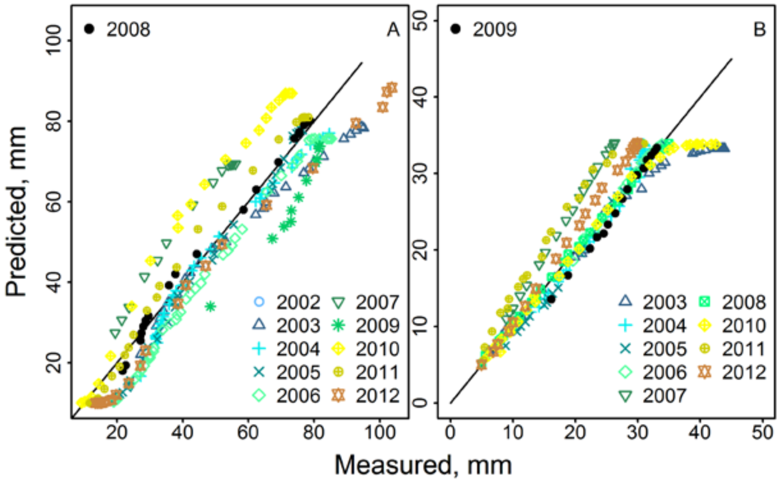

Figure 10. Measured and predicted shoot length (A) and needle length (B). The black line represents 1:1 and the black dots the year used for parameter estimation.

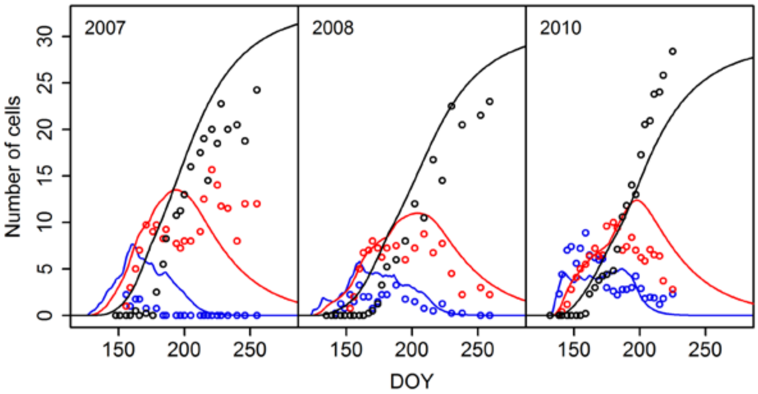

Figure 11. Actual measured (open dots) and predicted (lines) data indicate the numbers of enlarging, wall forming and mature tracheids (blue, red and black, respectively). DOY stands for day of the year for the years 2007, 2008 and 2010.

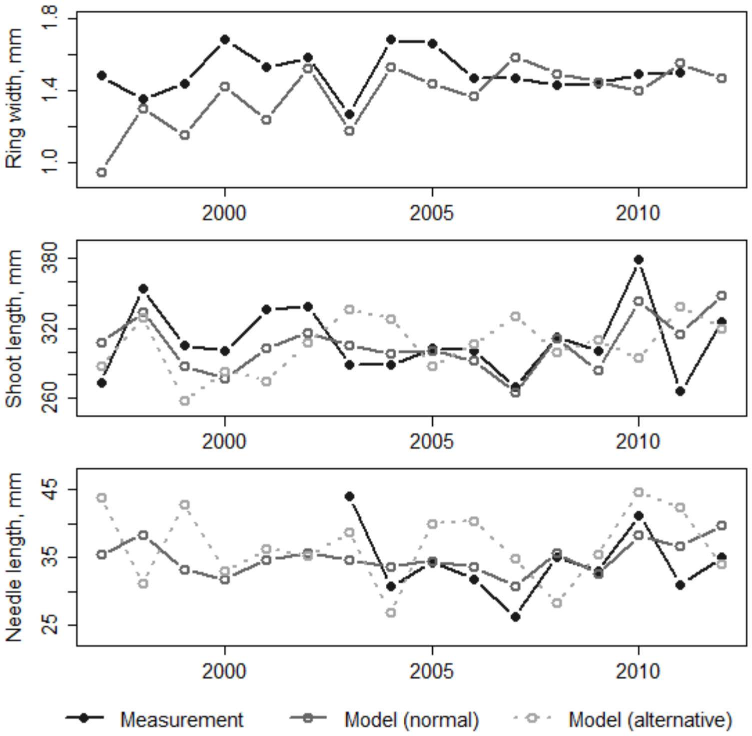

Figure 12. Measured and modelled inter-annual variation of ring width and shoot and needle length during the 1997-2012 period. Model (normal) is as found in model description (CASSIA, **II**). In model (alternative) shoot length depends on temperatures of the preceding year and needle length depends on the temperatures of the current year (instead of GPP of the preceding year).

Carbon assimilation and consumption are not concurrent processes throughout the year. Whereas carbon assimilation exceeds the consumption of carbon for growth and respiration during early spring and late summer, carbon consumption is larger than its assimilation during midsummer's intense growth period and from late autumn to early spring due to restricted photosynthesis (**II**, Fig. 13).

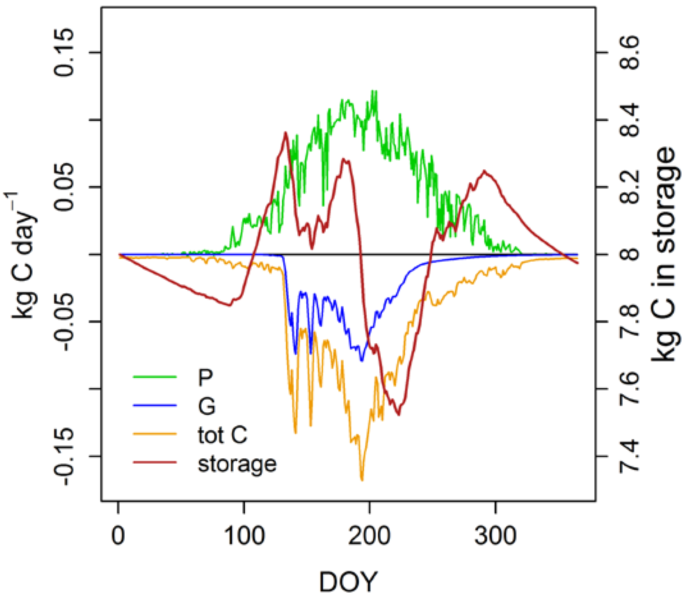

Figure 13. Photosynthesis (P), carbon consumption for growth (G), total carbon consumption (tot C) and stored C (storage) in year 2010. DOY stands for day of the year.

DISCUSSION

The effect of temperature on the timing and rate of growth

The results of this study indicate that lower temperatures than the previously reported 3-10 ºC range in tissue development generally (Körner 1998) or the 5.6-8.5 ºC range for the activity of xylogenesis (Rossi et al. 2007, 2008, Deslauriers et al. 2008) are sufficient for development progression to occur (**III**). Kanninen et al. (1982) used different temperature responses for describing ontogenetic development and growth. Their idea is parallel to the "chilling days" and "forcing days" concepts that were introduced by Cannel and Smith (1983) and used by e.g. Linkosalo et al. (2008) and Viherä-Aarnio et al. (2014). This kind of approach could improve the reliability of growth onset prediction in the CASSIA model. The results of this present study and the results reported in the studies cited above suggest that the onset of growth occurs as a continuous process that is determined by temperature accumulation during spring. In regions with highly varying spring temperatures, the onset of growth cannot be determined from momentary temperatures (**III**).

The predicted responses of growth to temperature differ in different models especially at low temperatures (see Fig. 2 and the related references). This may introduce a significant bias in modelling the growth onset when temperatures stay low for a long period. Jyske et al. (2014) observed that the temperature sum (with threshold temperature +5 °C) needed for secondary growth onset varies largely between study sites (environmental conditions) and years, which indicates that a temperature sum model alone is too simple a model for describing growth onset in different locations or habitats. In this study, however, CASSIA predicted the onset of needle, primary, and secondary growth during the measurement years to a satisfying level using the simple temperature response model. Day length was implicitly taken into account as the calculation of the temperature accumulation (*s*) was initiated from March 20 (DOY = 79) for secondary growth (**II**).

The effect of temperature and other environmental factors on growth cessation is even more complex and unclear than their effect on the onset of growth (Olsen 2010). In this study, the growth of new shoots and also in some years the growth of needles had already ceased before the warmest period of the year and long before low autumn temperatures were encountered. The CASSIA model managed to predict shoot growth cessation based on the temperature sum (**I, II**). The cessation of needle and tracheid growth during the measurement years was also successfully predicted by the CASSIA model. However, day length and water availability have also been reported to affect the timing of growth cessation (Wareing 1956, Koski and Sievänen 1985, Hänninen et al. 1990, Ziaco and Biondi 2016) and especially autumn senescence and the fall into dormancy (Way 2011). The determination of the cessation of growth is species-specific (Koski and Sievänen 1985, Rhode et al. 2011) and organ-specific as the driving factors for e.g. shoot growth and root growth as well as the length of their growth periods differ significantly (Fig. 8).

Environmental control of growth is thus complex because 1) the effects are process- and organ-specific but the processes and organs are, nevertheless, related to each other as discussed above and 2) they exert effects at multiple time scales. First, temperature has an instantaneous effect, which produces the day-to-day variation in growth ($g(t)$ in eq. 4, Fig. 3). Second, environmental factors drive the phenology which can be described as temperature (or other factor) accumulation during the whole non-dormancy period (Sarvas 1972, $f_i(s_i(t))$ in eq. 4). Third, environmental factors have delayed effects at various time scales. The delayed effect is most obvious for shoot growth, where the first part of the growth (bud formation) occurs in one year and the second (shoot elongation) in the next year, partly determined by the first year. Delayed effects have also been reported for secondary growth (Vaganov et al. 2009, Korpela et al. 2011, Babst et al. 2013).

Throughout a year, photosynthetic production and temperature are related to each other and therefore it can be stated that GPP could explain the short term growth variations as well as temperature. This possibility was considered while structuring the model. The correlation between temperature and GPP was, however, rather weak during the growth period and the relationship between growth and GPP weak compared to relationship between growth and temperature (Fig. 14).

Along with climate change, either the timing of growth onset or its cessation or both are predicted to move earlier or later (Menzel and Fabian. 1999, Way et al. 2011). Consequently, if the change is not similar for both, then the length of the growth period(s) will change. Growth cessation of many tree species with a predetermined growing habit occur at a certain stage of temperature accumulation (Sarvas 1972, Salminen and Jalkanen 2007), thus acclimatization or adaptation is needed to efficiently exploit the longer growing seasons (periods with favourable temperatures). In study **I,** the high temperatures encountered in late summer led to later growth cessation of shoot growth (in thermal time units) in the following summer, which is one mechanism of utilizing longer growing seasons. Furthermore, high autumn temperatures have resulted in later bud burst in the following spring with *Betula* and *Alnus* species, which could counterbalance the effect of warm springs that hasten bud burst (Heide 2003).

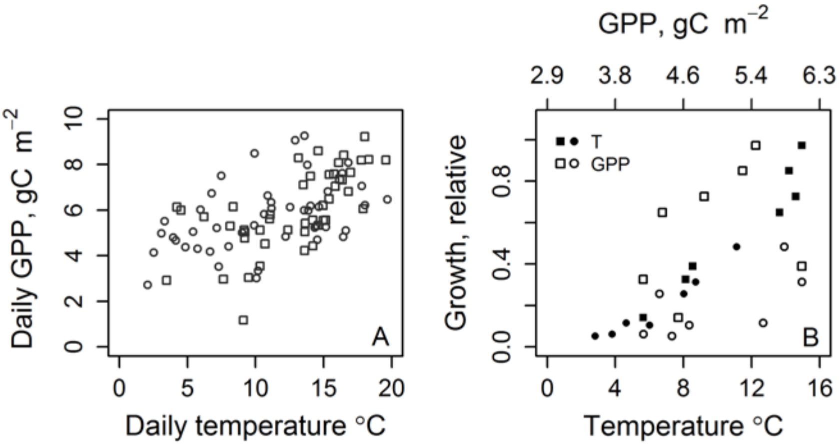

Figure 14. A) The relationship between daily average temperature and daily GPP during the shoot growth period (1.5.-15.6.) of two years. Squares represent year 2002 and circles year 2008. $R^2_{2002} = 0.42$. $R^2_{2008} = 0.22$. B) The relationship between measured growth and temperature (filled symbols) or GPP (open symbols) during the latter half of May, when the effect of phenology on shoot growth can be considered rather stable. Years as in (A).

Interrelations of the growth dynamics of different tree organs

Shoot growth phenology is easy to observe, therefore it would be convenient to be able to relate the beginning of growth of other tree organs to that of shoot growth. Of course this is the case only when there are actual mechanisms and processes that lead to these interrelationships and not simply correlations that may change in respect to environmental conditions. Such an apparently harmonious effect would be possible, if growth onset depends on temperature accumulation (or other factors) in every organ in a similar way. There was a relationship found between the onset and early part of needle and shoot growth (**III**). There may, however, not be such a direct relationship between the onset of shoot growth and growth of other organs (Steinaker et al. 2010, Delpierre et al. 2016a). Huang et al. (2014) were able to model secondary growth onset with observations of cambium activity, bud/shoot phenology and needle growth, which is a step forward in combining the growth of different organs. However, this also reinforces the statement about the complexity of the whole tree modelling. Furthermore, modelling growth cessation of tree organs may even be more difficult to combine or not even justified when the driving factors of growth cessation vary among organs (see above).

Primary growth in southern Finland begins in late April to early May depending on spring temperatures and typically continues until late June. According to the results of this study, needle growth begins almost concurrently with shoot growth (**III**) although this is not measurable from outside the bud until early June. Secondary growth (defined as first new enlarging tracheids) begins in late May and lasts until late July (new cell formation) or late autumn (cell wall formation) (**II**, Fig. 11). Measurements of root phenology are limited (Du and Fang 2014, Delpierre et al. 2016a) but root growth is strongly affected by soil temperature and moisture (Bowen 1970, Valdés et al. 2006) and it continues until autumn if conditions are favourable (Puhe 2003, Steinaker et al. 2010). The lengths of the growth periods as presented here thus vary from two months (primary growth) to four months (secondary growth, root growth) (**II**, Fig. 8). However, primary growth probably also continues as cell wall thickening and lignification for some period after the cessation of length growth. That is, among others, a factor that should be quantified in order to model the timing of carbon consumption as realistically and accurately as possible.

Source and sink effects on growth

Sink-source dynamics are being studied widely (Wiley and Helliker 2012, Palacio et al. 2014, Fatichi et al. 2014, Guillemot et al. 2015). A more comprehensive understanding of sink-source dynamics is important for being able to determine how growth and carbon balance and consequent productivity of forests change when the possible limiting factors vary (Medlyn et al. 2011). The predictions of changes in carbon balance depend on the underlying assumptions of growth restricting factors.

The activity of both the photosynthetic production and the growth sink (described by using some kind of a model) depend on direct and indirect effects of environmental factors. Whether the limiting environmental factors exert their effects via sink or source is in many cases difficult to ascertain, because many of the factors that restrict the growth sink also decrease photosynthesis (Tardieu et al. 2011, Wiley and Helliker 2012, Körner 2015). However, the response of on one hand photosynthesis and on the other hand growth to environmental factors differ especially at low temperature or moisture conditions (Palacio et al. 2014, Delpierre et al. 2016b). The effect may also vary according to e.g. the phenological state of the tree or stress conditions. An example of the stress conditions was described by Handa et al. (2005) when they observed that CO_2 addition to healthy evergreen trees did not increase growth although photosynthesis was enhanced, whereas partly defoliated trees showed a positive growth response to CO_2 increment.

Source limitation in CASSIA occurs in two ways. First, the direct short-term effect of storage (variable *k*, eq. 5) reduces growth when the storage level decreases below a threshold level. This effect was minor during the study period. The only years the value of *k* was below 0.95 for more than 20 days were years 2006 and 2010, when prolonged rainless periods combined with high evaporation demands reduced photosynthesis. However, even in those "drought" years the daily value of *k* stayed over 0.91 at all times). Second, maximum growth (parameter *L*, eq. 4) depends on carbon source (GPP) of the previous year (primary growth and needles) or ongoing year (secondary growth). These assumptions caused between-year variation to the modelled growth that was close to the measured variation (Fig. 12). This is also in accordance with the finding that a current year's carbon availability affects the new ring width and the number of produced tracheids (Babst et al. 2014, Deslauriers et al. 2016).

The results reported by Junttila and Heide (1981) indicate that in the most northern parts of Finland and Norway the temperature of previous and current growing season for shoots and needles, respectively, would be the factors determining total dimensional growth instead of GPP. The alternative determination of the shoot or needle length maximum growth with temperature in this study did not, however, lead to satisfying results of between year variation (Fig. 12, alternative model). This could indicate that in the northernmost regions temperature becomes even more limiting than at the site used for this study.

Our results indicate that the combined effects of source and sink limitations determine the growth (**II**) instead of separate source or sink limitation. A simplified assumption would be that growth is sink limited on short time scales (days) under normal conditions but would be source limited on longer timescales (years). The sink limitation on short timescales is supported by the success in modelling the daily growth variation solely based on temperature, whereas over longer time scales growth was enhanced or restricted by actualized photosynthetic production. The assumption of complex sink–source interactions is also supported by the results reported by Sveinbjörnsson et al. (2010), Guillemot et al. (2015) and Deslauriers et al. (2016).

Different types of sink limitation may occur on different temporal scales. One such limitation could function in such a way that temperature determines the momentary growth rate in relation to maximum growth rate. This in turn, would be determined by other factors such as the availability of nutrients or assimilated carbon. The environmental factors that produce sink limitation are temperature and water, nutrient and light availability (see Fatichi et al. 2014). Of these factors, the effects of temperature are mainly considered in the CASSIA model, although the effect of light on growth onset and the effect soil moisture on root growth are also included in the model. There are three reasons for mainly focusing on temperature rather than the other factors in our model: 1) Temperature is the most important environmental factor in boreal forests. 2) Droughts have been extremely rare at our study site. 3) Nutrient availability can be considered relatively constant at a single site over the study period. However, the other factors do and will become highly important when predicting growth on other site types or simulating future climate conditions. Thus, the effect of water limitation should be added to CASSIA as a factor that imposes a direct limitation on growth sink strength even before it affects growth indirectly via photosynthesis (Hölttä et al.

2010, Deslauriers et al. 2016). Nutrient effect on growth could be included in maximum daily growth (*L*) (Bergh et al. 1999) and possibly phenology (Sigurdsson 2001).

The NSC storages of starch and soluble sugars level-off the short-term differences between carbon assimilation and consumption (Palacio et al. 2014). The sink–source status of storages is dual: during abundant carbon assimilation the storage acts as a carbon sink but will become a carbon source later (Clifford 1992). Furthermore, the functionality of the storage is still a matter of discussion (Sala et al. 2012, Dietze et al. 2014). Currently, the role of storage in CASSIA is nearly passive, i.e. storage limits growth only when the amount of stored carbon falls below a certain threshold level. However, a storage of adequate size is important for providing a tree with a buffer against carbon starvation caused by stress conditions such as drought or pest attack. This could imply that storages act as equal sinks to those of growing organs (Sala et al. 2012). Thus, in carbon limited conditions carbon would be directed to storage to prevent the storage from depleting. As a consequence, growth would be reduced via reduced relative sink strengths even if the level of storage didn´t reduce. In addition, high NSC levels in leaves due to restricted transport of sugars, have been shown to down-regulate photosynthesis (Nikinmaa et al. 2012). To what extent the NSC storages are passive (purely balancing the discrepancies between assimilation and consumption) or active (equal allocation target of carbon with growth etc.) remains an open question. Therefore, the activity/passivity of the storages and the factors driving carbon fluxes to or from the storages have to be studied further (Delpierre et al. 2016a).

Future improvements and possibilities of CASSIA

In addition to those mentioned in the previous sections there are aspects in the model that can and should be improved in the future or adapted when used for other species or purposes.

Two of the four organs were studied in detail in this research (shoots (**I**), needles (**III**)). The need for and the difficulties of using a more accurate root growth model were discussed in the previous sections. However, with the method introduced by Nakano et al. (2012) where root growth is scanned at regular intervals with a scanner installed into the soil, we will hopefully be able to quantify the effects of environmental effects on root phenology and growth in the near future. More complex and sophisticated models have been introduced to describe secondary growth (Hölttä et al. 2010), which will serve more detailed purposes. A more mechanistic approach to the complex processes of growth would, however, improve the reliability of this model in different conditions and the inclusion of e.g. the variations in tracheid dimensions as a factor would help in interpreting the effects environmental factors.

At this stage of the model’s development only one year at a time has been considered and the only lagging effects are the influences of previous summer GPP on L_S and L_N). This means setting the storage to the initial value at the beginning of each year. Doing so avoids errors in the interpretation of the results of source and sink factors on growth, which could otherwise be caused by inaccuracies in the storage compound or other parts of the carbon balance. Furthermore, no senescence processes were included into the CASSIA model. This was suitable for studying the intra- and inter-annual effects of source and sink limitations on growth. However, when studying for a longer period, the following aspects must be considered:

1) The storage compound must be continuous. This implies verifying the model predictions of seasonal change with direct measurements of stored carbon and also reconsidering the way in which carbon is directed to storage or translocated from

storage for other purposes (active vs. passive storage). There may also be differences in the amounts of carbon used from different storage organs e.g. NSC in shoots vs. roots (Mei et al. 2015).

2) The functional structure of the tree must be maintained during a long period (Mäkelä and Valentine 2006).
3) The needle and fine root senescence variables must be added to the model.
4) Age related trends related to e.g. length growth must be considered.
5) Possible changes in forest nutrition, such as nitrogen deposition or mineralization (see Eastaugh et al. (2011) for effects of increased nitrogen deposition), or structures that enhance or decrease growth and photosynthesis should be taken into account. Duran et al. (2016) predicted decreasing nitrogen mineralization with climate change in cold areas, even though generally increased temperature actually enhances mineralization of nitrogen (Bagerzadeh et al. 2008).

The dynamic structure and inherent flexibility of CASSIA enable it to be adapted for modelling growth of different tree species after adequate modification to species-specific parameters and/or functions. There are fundamental differences in the growing habits of different tree species and thus, their response to environmental factors (see above) and source–sink limitation strategies differ (Handa et al. 2005, Huang et al. 2014, Guillemot et al. 2015). Therefore studying how different conditions limit or enhance the rates of carbon assimilation and consumption and affect their timing within a year would be of interest and relevance. For example, a linear time or a combined linear and temperature time approach can be considered, instead of the thermal time approach for regulating the onset and cessation of growth in trees with free (instead of predominant) shoot growing habit (Koski and Sievänen 1985).

CONCLUDING REMARKS

The aim of this study was to define the effects of temperature on the phenology and growth rate of Scots pine organs and further to examine carbon source and sink effects on growth from the point of view of carbon balance. It was shown that the within year growth variation of shoots and needles in addition to the formation of new secondary cells could be explained by short term and long term changes in temperature, which indicates a sink limitation of growth. On the other hand, carbon source (photosynthesis) in certain time periods explained the between years growth variation of the same tree organs. The study was conducted at only one site in Finland but the results give insights into the possible general mechanisms regarding the determination of growth and carbon use. With adequate modifications, the CASSIA model is also applicable to other tree species and areas due to its dynamic structure.

Although the issue has been studied intensively, a multitude of open questions remain regarding the processes of carbon consumption and assimilation. Hadden and Grelle (2016) observed that the temperature responses of respiration at low temperatures in northern Sweden have increased from years 1997-2009 to years 2010-2013, which has led to increased total ecosystem respiration whereas GPP did not change during the years 1997-2013. In turn, Atkin and Tjoelker (2003) and Drake et al. (2016) showed that the long term respiration of trees acclimatizes to increasing temperatures but the extent of this is unknown. Similar uncertainties can also be related to photosynthesis (Luo 2007). Although the uncertainties concerning growth determination are even larger, the analysis conducted in study **II** provides tools for comparing the source and sink limitations of growth. This is of considerable importance for understanding the tree functionality and carbon balance as well as predicting their alteration in the future. Studies **I** and **III** revealed temperature effects that are important for understanding the phenology of different organs, which is also of increasing interest (Linkosalo et al. 2000, Caffarra and Donnelly 2011) as growth timing acts as a notable part of carbon balance.

Schwalm and Ek (2001) compiled general requirements for models in order for them to be applicable for use in a changing environment. Those authors stated that we need comprehensive modelling work to identify the study areas where more knowledge is required. Growth of a tree is affected by a complex combination of environmental factors and source and sink processes, which act on different temporal scales. We need to be able to describe fully the real causalities behind these processes instead of barely describing correlations to attain justified predictions over a long time scale (Delpierre et al. 2012, Fatichi et al. 2014). In conclusion, the question of determining the limiting factor of growth remains unanswered. However, a step forward has been taken both in identifying gaps of knowledge and in revealing connections between the environmental and other factors and growth processes.

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