

Physiological growth model CASSIA predicts carbon allocation and wood formation of Scots pine

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Highlights: The dynamic, intra-annual model CASSIA combines detailed models of wood formation and properties with a process-based growth simulation system. It predicts the daily growth of wood, needles, shoots and roots of Scots pine based on weather variation and photosynthetic production.

Keywords: dynamic modeling, *Pinus sylvestris* L, sink, source, xylogenesis

INTRODUCTION

The growth of trees varies according to genetic origin, tree age and environmental drivers like tree position in the stand, the weather conditions of the current and previous years, and soil characteristics (Oleksyn et al. 2001, Salminen and Jalkanen 2005, Chuine et al. 2006, Pinto et al. 2011). Mechanistic understanding of the external and internal control of growth is needed to understand the effects of changing environment on tree growth and wood formation. Drew et al. (2010), for example, has developed a process-based approach to model wood property variation but dynamic model CASSIA (Carbon Allocation Sink-Source Interaction Analysis) is one of the first attempts to combine detailed models of intra-annual wood formation (xylogenesis) with a process-based growth simulation system in a whole-tree carbon balance framework. It predicts the daily growth of wood, needles, shoots and roots of Scots pine (*Pinus sylvestris* L.) based on weather variation and photosynthetic production. It also includes a description of wood formation at time scales ranging from days to several years, in a whole-tree carbon balance framework. Especially, the model is able to describe how the sink and source relationships interact through various time scales in tree growth.

THE MODEL

In the model, the state variables are the storages of short chain sugars (sucrose), long chain sugars (starch), and the biomasses of needles, primary wood, secondary wood and fine root (Fig. 1). The model further divides the cambial growth to enlarging, wall forming and mature tracheids. The model projects the states of growth at any point in time with a time step of one day.

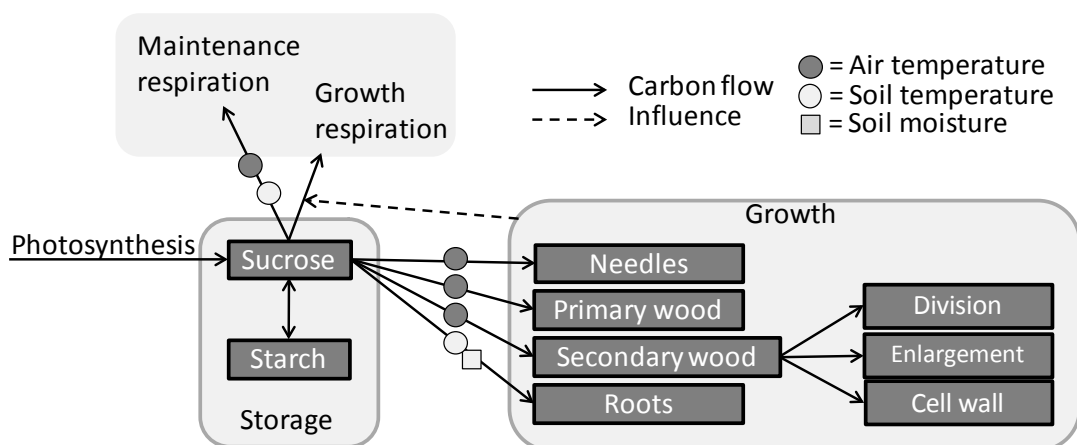


Fig. 1. A schematic presentation of the model. The photosynthesis is the source of carbon whereas the growth of needles, wood and roots and respiration act as carbon sinks. The arrows represent flows of carbon and the shapes stand for the environmental effects of factors.

The daily change in the pool of sugars without the exchange between sucrose and starch storages (dS/dt , g C day⁻¹) depends on photosynthesis, $P(t)$, and maintenance respiration, $R^M(t)$, growth, $G^{tot}(t)$, and growth respiration, $R^G(t)$:

$$\frac{dS}{dt} = P(t) - R^M(t) - G^{tot}(t) - R^G(t), \quad (1)$$

The photosynthesis, $P(t)$, is calculated according to Mäkelä et al. (2008). The maintenance respiration, $R^M(t)$, depends on the biomass and ambient temperature that is the air temperature for the aboveground parts and soil temperature for the roots. The empirical temperature dependence of each part is obtained from continuous measurements at the SMEARII station. The growth respiration, $R^G(t)$, is linearly dependent on growth according to Running and Coughlan (1988).

The potential growth i.e. growth sink is based on external environment. The most important environmental factor for the above ground growth is the air temperature whereas soil temperature and moisture determine the potential growth of roots. The potential growth follows the annual cycle of tree activity in terms of thermal time, which is assumed to progress with daily mean temperature (Hänninen and Kramer 2007). In the model, the thermal time is an accumulation of a sigmoid function of temperature (Hänninen 1990). The active growth period begins and ends when the accumulation of thermal time reaches threshold values. The level of growth proceeds with the accumulated thermal time as a sine function for shoots, needles and roots whereas the cambial growth follows a square root function of the accumulated thermal time.

The potential growth occurs when carbon is not a limiting factor, i.e., sink strength regulates the growth. If photosynthetic input exceeds the sinks, the sugars are converted and stored as starch. The carbon storages are used to supplement the growth, if the carbon bound in photosynthesis is insufficient to cover the need of the sinks entirely. If the carbon storage is low, the growth becomes source-limited and it is lower than the potential growth.

MEASUREMENTS

We measured the tree growth in middle-aged Scots pine stands in Northern Finland at SMEARI (67°46'N, 29°35'E) and in Southern Finland at SMEARII (61°52'N, 24°17'E) and in Ruotsinkylä (60°21'N, 25°00'E). We took microcore samples at SMEARI and SMEARII during 2007–2009 and in Ruotsinkylä during 2002–2010 for the timing of tracheid formation and differentiation.

The length growth of needles and branches in different parts of the canopy were measured 2–3 times in a week during the growing seasons. Because measurements were not made every day, an average daily growth of the measuring days was calculated. The shoot growth was measured in SMEARI during 2007–2009 and in SMEARII in 2003–2009. Needle growth was measured at SMEARII in 2003–2009.

We estimated the model parameters using the measurements in SMEARII in 2008 and used them for the model runs of the other sites and years.

PRELIMINARY RESULTS

The model runs for SMEARII during 2002–2009 reveal that the growth was mainly sink-driven, except for the late growing season in 2006 and the early season in 2007. The growth was suppressed by a prolonged drought in August 2006 that decreased the photosynthetic input.

The model succeeded to predict the growth of shoots (Fig. 2A) in years 2006, 2008 and 2009, whereas in years 2005 and 2007, the onset and cessation were consistent with the measurements but the final shoot length was overestimated. In general, the model succeeded to predict the timing of growth (Fig. 2B) and average final length of needles, apart from years 2005–2007 when the model accurately estimated onset and growth cessation but overestimated the final needle length. Moreover, the model succeeded to predict the dynamics of cambial growth (Fig. 2C), except for the year 2009, when the estimated number of cells was lower and the onset of cambial growth later than the observed ones.

With the parameters estimated for SMEARII stand in year 2008, the model succeeded to predict the timing of cambial growth in Värriö and in Ruotsinkylä in years 2007–2008 but in year 2009, the model resulted in an underestimation similar to Hyytiälä in 2009. The model accomplished to predict the final ring

width in Värriö, but in Ruotsinkylä that is a more fertile site, the model underestimated the final ring width indicating a need to tune the fertility-specific parameters.

In future, we will develop the model by refining the description of uptake, allocation, and transport processes of sugars and water within trees to improve understanding of stress responses, especially the effects of prolonged drought on tree growth.

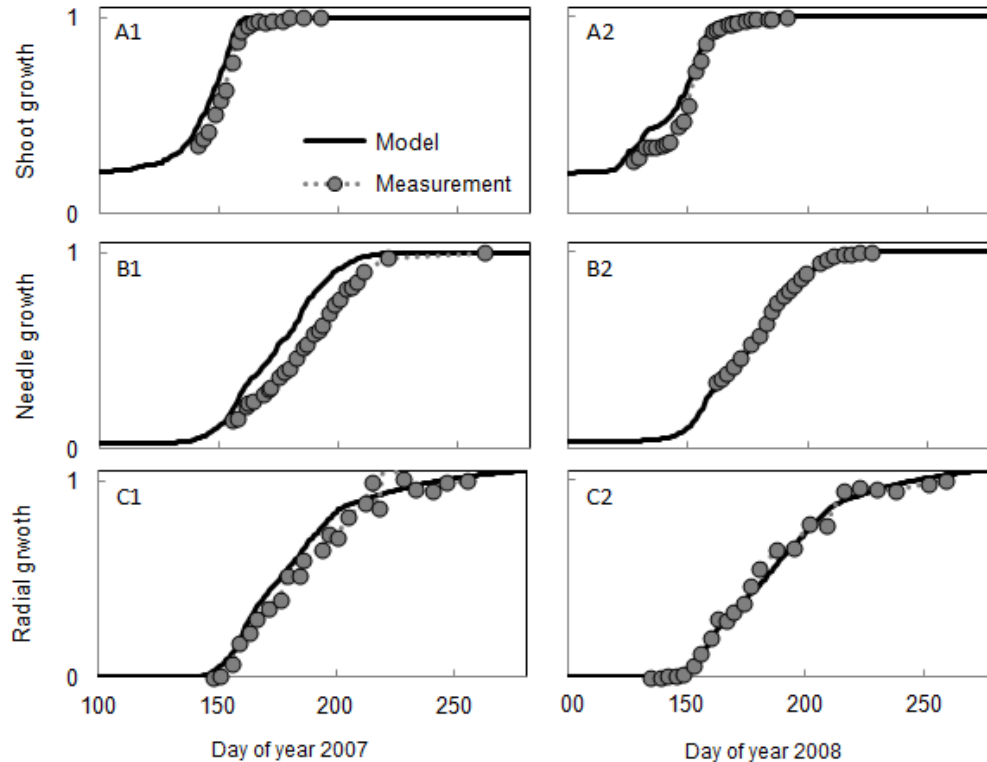


Fig. 2: The modeled (lines) and measured (circles) daily average relative growth of shoots (A1-A2), needles (B1-B2) and the stem radius (C1-C2) at SMEARII in 2007 (left panels) and in 2008 (right panels).

LITERATURE CITED

- Chuine I, Rehfeldt GE, Aitken SN. 2006.** Height growth determinants and adaptation to temperature in pines: a case study of *Pinus contorta* and *Pinus monticola*. *Canadian Journal of Forest Research* **36**: 1059-1066. doi:10.1139/X06-005
- Drew DM, Downes GM, Battaglia M. 2010.** CAMBIUM, a process-based model of daily xylem development in Eucalyptus. *Journal of Theoretical Biology* **264**: 395-406
- Hänninen H. 1990.** Modeling dormancy release in trees from cool and temperate regions. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A. & Warren, W.G. (eds.). *Process modeling of forest growth responses to environmental stress*. Timber Press, Portland p. 159-165.
- Hänninen H, Kramer K. 2007.** A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva fennica* **41**(1): 167-205.
- Mäkelä A, Pulkkinen M, Kolari P, Lagergren F, Berbigier P, Lindroth A, Loustau D, Nikinmaa E, Vesala T, Hari P. 2008.** Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology* **14**: 92-108. DOI: 10.1111/j.1365-2486.2007.01463.x
- Pinto CA, Henriques MO, Figueiredo JP, David JS, Abreu FG, Pereira JS, Correia I. 2011.** Phenology and growth dynamics in Mediterranean evergreen oaks: Effects of environmental conditions and water relations. *Forest Ecology and Management* **262**: 500-508. doi:10.1016/j.foreco.2011.04.018
- Oleksyn J, Reich PB, Tjoelker MG, Chalupka W. 2001.** Biogeographic differences in shoot elongation pattern among European Scots pine populations. *Forest Ecology and Management* **148**: 207-220. DOI: [http://dx.doi.org/10.1016/S0378-1127\(00\)00537-5](http://dx.doi.org/10.1016/S0378-1127(00)00537-5)
- Running SW, Coughlan JC. 1988.** A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling* **42**: 125-154.
- Salminen H, Jalkanen R. 2005.** Modelling the effect of temperature on height increment of scots pine at high latitudes. *Silva Fennica* **39**(4): 497-508.