Wood formation under varying environmental conditions (WOVEN)

FINAL REPORT

Title of the research project	Wood formation under varying environmental conditions
Coordinator of the project	Harri Mäkinen

BASIC PROJECT DATA

Project period	01.01.2008-31.12.2011
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Name, degree, job title	Sex (M/F)	Organization, graduate school	For a visitor: organization & country of origin	Funder
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DEGREES
Degrees earned or to be earned within this project.

Year	Degree	Sex (M/F)	Name, year of birth and year of earning M.Sc., D.Sc., etc. Degree	University	Supervisor of thesis, supervisor's organization
2011	Dr	M	Tuomo Kalliokoski, 1978, 2003 M.Sc.	University of Helsinki	Dr. Risto Sievänen, Finnish Forest Research Institute
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ABSTRACT

The WOVEN project deepens our understanding of the factors affecting wood formation and the variation in wood properties of Norway spruce and Scots pine. We studied, with the help of empirical observations and mechanistic models, the production and the allocation of carbohydrates, and the dynamic interplay between environmental and genetic factors as they affect cambial activity.

To accomplish these objectives, we analysed:

(1) the effects of weather variables on wood formation, fibre characteristics, and chemistry,

(2) the effects of genetic origin on wood formation,

(3) the factors controlling the seasonality in carbon assimilation and availability of current and stored photosynthates during the growing season, and their relationship to nitrogen availability,

(4) the effects of water relations and nutrient status on xylem and phloem transport and wood formation, and

(5) formulated a dynamic process-based model describing wood formation in terms of whole-tree physiology.

1.1 Introduction

1.1.1 Background

Climate change is expected to increase forest production and therefore the wood raw material supply, although several uncertainties remain, especially related to extreme climate events potentially causing large-scale forest damage. In order to assess the adaptive capacity of forest management to the anticipated changes in forest production and demand for wood raw material, we need to understand the consequences of different management choices on the raw material supply in interaction with wood properties.

Stem growth can be defined as an increase in the number and size of xylem cells through the activity of meristematic tissues. Despite of the basic nature of the process, our knowledge concerning the timing and rate of the subsequent phases of wood formation is very limited, even for the most important European tree species. An important factor behind the gaps of knowledge is the difficulty in measuring wood formation at short intervals. Methods based on sampling and measuring the newly formed xylem (microcoring, FT-IR spectroscopy) have recently improved.

1.1.2 Objectives

The aims of this project were to deepen our understanding of the factors affecting wood formation and the variation in wood properties of Norway spruce and Scots pine. We studied, with the help of empirical observations and mechanistic models, the production and the allocation of carbohydrates, and the dynamic interplay between environmental and genetic factors as they affect cambial activity. To accomplish these objectives, we (1) analysed the effects of weather variables on wood formation, fibre characteristics, and chemistry, (2) analysed the effects of genetic origin on wood formation, (3) studied the factors controlling the seasonality in carbon assimilation and availability of current and stored photosynthates during the growing season, and their relationship to nitrogen availability, (4) analysed the effects of water relations and nutrient status on xylem and phloem transport and wood formation, and (5) formulated a dynamic process-based model describing wood formation in terms of whole-tree physiology.

1.2 Results and discussion

Timing and rate of xylem formation were analysed throughout the growing seasons in Finland, Sweden, and Norway. Artificially induced drought during four to five consecutive growing seasons caused a small reduction in both radial and height increment in mature Norway spruce. The reduction in radial increment was due to a smaller number of both early- and latewood tracheids. The drought-treatment caused only small changes in the anatomy of the wood. In a artificial soil frost experiment, delayed thawing of moraine soil had only a small impact on the onset, timing and duration of cambial activity in Norway spruce. In a provenance experiment, differences between the provenances in the onset, highest daily rate, and cessation of tracheid formation were small, in contrast to large between-year variations in the timing of cambial activity.

In the Finnish National Forest Inventory (NFI), thousands of trees are cored every year during the growing season. We demonstrated that NFI ring-width data can be applied for analyzing the intra-annual progress of radial increment. Major differences in the progress of radial increment were neither found between Scots pine and Norway spruce nor between the southern and middle boreal zone. There were, however, large between-year variations. The rather similar progress of radial increment in the both climatic zones suggests that there are growth regulating factors that are common for the entire area.

Dendrometers are devices for measuring the stem radius of a tree continuously. We studied the use of logistic and generalised logistic models for exploring dendrometer data and for automatically determining the onset and cessation dates of radial increase. We used data measured in two stands in southern Finland to test the performance of the models. The generalised logistic models performed well compared to earlier approaches. In addition, the exploratory analysis revealed distinct differences between growth patterns of trees in different calendar years.

Tree-ring indices have traditionally been analysed utilising monthly mean climate data. In northern Finland, we utilised higher resolution data – daily mean temperatures as well as estimated daily photosynthetic production – in analysing growth variations. Our results suggest that the most influential temperature period begins in late June and extends nearly to the end of July. During the middle part of the growing season, estimated daily photosynthetic production produced slightly weaker correlations with growth indices than did temperature.

Wood samples were taken from two sites around Vindeln, Sweden (Flakaliden and Rosinedal) from several plots (including both control and fertilised) at each site. FT-IR microscopic measurements of thin cross-sections of these trees (both spruce and pine) were carried out. Results indicated differences in chemical composition between control and fertilized trees, with both relative lignin and cellulose amounts influenced. In addition, different regions from early to latewood within an annual ring were markedly different in chemical composition, as well regions of different annual rings. That is, early wood cells formed during one year can be differentiated from early wood cells of another year, based on the FT-IR spectra, i.e. chemical composition.

Based on these findings, and because the trees used for these samples were the same ones as were used for microcoring, dating of cells and correlating chemical changes to environmental variables looks feasible and is under way.

In the Swedish stands, the compartmental fluxes of carbon were measured, as well as the total carbon exchange by means of eddy covariance technique. Analyses of the samples from the pulse-labelling experiments established in a young Scots pine stand, with CO_2 enriched with C-13, is in progress and the first papers have been published. In collaboration with Australian colleagues, a new pulse-labelling experiment with CO_2 enriched with C-13, was performed on *Eucalyptus saligna* trees, grown at ambient and elevated [CO_2] in the whole-tree chambers previously used at Flakaliden. The analyses of this experiment is in progress, but is delayed because of limited capacity of C-13 analyses in Australia.

Wood samples and field measurements of growth and exterior quality characteristics were collected from progeny and clonal experiments along a climatic gradient from west Norway to east Finland. The families and the clones express large variation in phenology, which is important for climatic adaptation. Wood density for individual rings was analysed in relation to phenology and climatic data. The material consists of 6000 increment cores. The x-ray computer tomography scanning (CT-scanner) method was improved to facilitate automatic feeding of samples into the scanner, as well as to obtain CT-values (density values) extracted from the computed images after scanning. The wood samples were measured. The results show that wood density is under strong genetic control and that there are little genotype by environment interactions. Hence, families and clones seem to perform relatively stable across different environments. Further analysis of the data will be focused on studying if there are relationships between bud phenology and wood density.

In one of the clonal trials, microcores from a sub-sample of the clones were sampled weekly through one growing season. The samples were prepared for microscopy studies to quantify the rate and stage of development of xylem. The results show that there are significant genetic variation in the rate of xylem formation. The clones sampled show contrasting bud phenology, some are early flushing while others are late flushing in the spring. Further analysis will reveal if there are phenotypic and genetic relationships between timing and rate of xylem formation and bud phenology.

Cambial growth was modelled as a function of detailed levelled physiological processes for cell enlargement and water and sugar transport to the cambium. Cambial growth was described at the cell level, where local turgor pressure and sugar concentration induce irreversible cell expansion and cell wall synthesis, respectively. It was demonstrated how transpiration and photosynthesis rates, metabolic and physiological processes, and structural features of a tree mediate their effects directly on the local water and sugar status and influence cambial growth. Large trees were predicted to be less sensitive to changes in the transient water and sugar status compared to smaller trees as they have more water and sugar storage and are therefore less coupled to short-term changes in the environment influencing photosynthetic production. However, they are more sensitive to soil drying. Modelling the cambial dynamics at individual cell level turned out to be a complex task as the radial short-distance transport of water and sugars and control signals determining cell division and cessation of cell enlargement and cell wall synthesis had to be described simultaneously.

A dynamic model of the tree carbon balance with a daily time step has been constructed. The carbon balance model of tree growth and wood formation was tested against the microcore measurements. The shoot and needle length growth sub-models were further developed and tested against a data set for eight growing seasons (2002 – 2009), and the dependence of the timing of growth on previous-year temperature was analysed. The timing of growth was also found to depend on the position of the shoot in the crown. Needle samples taken previously for measuring the development of the sugar content of needles during the summer were measured in the laboratory. Further data on other growth components were collected from the literature. These measurements were used for estimating parameters for the dynamic model. The model can be applied to analysing the within-year pattern of carbon fluxes and dimensional growth in trees. Our preliminary results suggest that the predictions compare well with empirical data from the SMEAR II eddy flux site.

The developed model was used to predict the effects of alternative climate change scenarios on the future growth trends of trees and wood properties. The consequences of alternative silvicultural options were also evaluated by simulations. The simulations enable comparison of different combinations of climate change scenarios and silvicultural regimes, including their effects on site specific water balance. Simulations revealed that similar drought as observed in 2006 has much more drastical consequences to growth than to photosynthetic production. While photosynthetic production was decreasing 5%, simultaneous decrease in stem growth was about 30%. This illustrates that estimation of yearly photosynthetic changes are not sufficient to correctly predict the influence of climate change on growth but we need to consider also the climatic influence on growth allocation.

1.3 Conclusions

Air temperature is a crucial factor which modifies the beginning, intensity and end of annual growth of trees. An increase in air temperature could favourably influence spring growth in the boreal forests which today feature a low average temperature, provided water supply is sufficient. Generally, a slight increase in air temperature can enhance rate of photosynthesis. Since respiration losses will also increase under increased air temperatures, net primary production will probably not increase as much as the rate of photosynthetic production. Often tree growth is, however, limited by other factors like tree water balance and availability of nutrients.

Under climate change scenarios the most endangered forest ecosystems will include Norway spruce forests outside their natural range at low elevations where evapotranspiration is high. Climate change, which has been predicted to increase the frequency of extreme drought and temperature events, may reduce Norway spruce growth also in the Nordic countries. Increased temperatures will enhance evapotranspiration, and early thawing of snow may lead to loss of water which may have been used later during the growing season. A longer growing season might not be fully utilised because of an overall lack of water and day-length control of growth cessation in autumn.

During the growing season, climate induced changes in temperature and precipitation patterns are unlikely to result in large changes in wood properties of Norway spruce. Moreover, Norway spruce seems to quickly recover from drought stress. Increased temperature during intermittent mild spells in late winter could, however, cause premature growth onset, and tree damage during subsequent frost periods may occur.

1.4a Capabilities generated by the project

The study is one of the first attempts to combine models of wood formation and properties with detailled process-based growth simulation models. Being based on the relationship between tree growth, environmental factors, and wood and tracheid properties, the approach is new, flexible and more general than most of the earlier simulation models. Thus, the applicability of growth models for predicting the effects of environmental factors, global change, and forest management, improves considerably. Simultaneous development of the process-based growth models and models for wood formation also enables one to test the model predictions against measured data on wood properties. The process-based growth models can be developed further in the future, and the theoretical approach used can be widened by parameterising it with the measurement data and explicitly comparing the model results with experimental data.

1.4b Utilisation of results

The project contributes to a detailed understanding of photosynthetic production, its dependence on the environment, the long-distance water transport in the xylem and phloem including substrate transport and utilisation, and their monitoring and dependence on tree structure.

Understanding the link between environmental factors and tree growth gives guidance for more sustainable forest management strategies in terms of the management of wood properties. The results can be used for predicting radial increment and wood properties under a changing climate and/or new management regimes. The scenarios include alternative forest management regimes and climate change scenarios. Silvicultural guidelines for producing desired wood properties can also be designed.

The results of the project help forestry practices to favour genotypes with proper adaptation to the prevailing climatic and edaphic conditions. Genotypes with traits that make trees more fit to increasing temperature and prolonged growing season can be selected to maximise carbon fixation and storage, but avoiding genotypes with high risks to abiotic or biotic damages. This is of great importance with tree species, like Norway spruce, which contain significant variation among populations of different geographical origins in terms of critical night length timing of radial and height growth, and metabolic events leading to frost hardiness.

Results may be used in planning of forest and environmental policy actions and means that help in mitigating and adapting to climate change. Thus, the project provides valuable input data for further studies assessing the economical and ecological impacts of climate change and alternative management regimes.

1.5 Publications and communication

a) Scientific publications

1. Articles in international scientific journals with peer review

Albaugh TJ, Bergh J, Lundmark T, Nilsson U, Stape JL, Allen HL, Linder S (2009). Do biological expansion factors adequately estimate stand-scale aboveground component biomass for Norway spruce? For. Ecol. Manage. 258: 2629-2637.

Brewer MJ, Sulkava M, Mäkinen H, Korpela M, Nöjd P, Hollmén J (2010). Logistic fitting method for detecting onset and cessation of tree stem radius increase. PLoS ONE (submitted)

Dieset A, Høibø OA, Skrøppa T, Steffenrem A. Timing and rate of xylem formation of four *Picea abies* clones showing contrasting bud phenology (tentative title). Manuscript in prep.

Gerten D, Luo Y, Le Maire G, Parton JW, Keough C, Weng E, Beier C, Ciais P, Cramer W, Dukes JS, Emmett B, Hanson PJ, Knapp A, Linder S, Nepstad D, Rustad L (2008). Modelled effects of multiple global change factors on ecosystem carbon and water dynamics in different climatic zones. Part I: precipitation-only effects. Global Change Biol. 4: 2365-2379.

Hall M, Räntfors M, Slaney M, Linder S, Wallin G (2009) Carbon dioxide exchange of buds and developing shoots of boreal Norway spruce exposed to elevated or ambient CO_2 concentration and temperature in whole-tree chambers. Tree Physiol. 29: 461-481.

Henttonen HM, Mäkinen H, Nöjd P (2009). Seasonal dynamics of wood formation of Scots pine and Norway spruce in southern and central Finland. Can. J. For. Res. 39: 606-618

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Hölttä T, Mäkinen H, Nöjd P, Mäkelä A, Nikinmaa E (2010). A physiological model of softwood cambial growth. Tree Physiol. 30: 1235-1252.

Hyvönen R, Persson T, Andersson S, Olsson B, Ågren GI, Linder S (2008). Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochem. 89: 121-137.

Jyske T, Hölttä T, Mäkinen H, Nöjd P, Lumme I, Spiecher H (2010). The effect of artificially induced drought on radial increment and wood properties of Norway spruce. Tree Physiol. 30: 103-115.

Jyske T, Kaakinen S, Nilsson U, Saranpää P, Vapaavuori E (2010). Effects of timing and intensity of thinning on wood structure and chemistry in Norway spruce. Holzforschung 64: 81-91.

Jyske T, Manner M, Mäkinen H, Nöjd P, Peltola H, Repo T (2011). The effects of artificial soil frost on cambial activity in Norway spruce. Manuscript in prep.

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Kalliokoski T, Reza M, Jyske T, Mäkinen H, Nöjd P (2011) Intra-annual tracheid formation of Norway spruce provenances in southern Finland. Tree Physiol (submitted)

Korpela M, Mäkinen H, Nöjd P, Hollmén J, Sulkava M (2010). Automatic detection of onset and cessation of tree stem radius increase using dendrometer data. Neurocomputing 73: 2039-2046.

Korpela M, Nöjd P, Hollmén J, Mäkinen H, Sulkava M, Hari P (2010). Photosynthesis, temperature and radial growth of Scots pine in northern Finland - identifying the influential time intervals. Trees (in print)

Kostiainen K, Kaakinen S, Saranpää P, Sigurdsson BD, Lundqvist SO, Linder S, Vapaavuori E (2009). Stem wood properties of mature Norway spruce after three years of continuous exposure to elevated [CO_2] and temperature. Global Change Biol. 15: 368–379.

Luo Y, Gerten D, Le Maire G, Parton WJ, Weng E, Zhou X, Keough C, Weng E, Beier C, Ciais P, Cramer W, Dukes JS, Emmett B, Hanson PJ, Knapp A, Linder S, Nepstad D, Rustad L (2008). Modelled interactive effects of precipitation, temperature, and CO_2 on ecosystem carbon and water dynamics in different climatic zones. Part II: interactive effects of precipitation, temperature, and CO_2. Global Change Biol. 14: 1986-1999.

Luyssaert S, Reichstein M, Schulze E-D, Janssens I A, Law BE, Papale D, Dragoni D, Goulden ML, Granier A, Kutsch WL, Linder S, Matteucci G, Moors E, Munger JW, Pilegaard K, Saunders M, Falge E M (2009). Toward a consistency cross-check of eddy covariance flux–based and biometric estimates of ecosystem carbon balance. Global Biogeochem. Cycles, 23: 13 pp.

Mäkinen H, Seo J-W, Nöjd P, Schmitt U, Jalkanen R (2008). Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. Eur. J. For. Res. 127: 235-245.

Schiestl-Aalto P, Nikinmaa E, Mäkelä A (2010). A model of daily shoot and needle elongation in Scots pine – temperature effects at different temporal scales. Submitted manuscript.

Skrøppa T, Johnsen Ø, Steffenrem A. Genetic variation in growth and growth rhythm traits in two short term tests from a factorial cross with Norway spruce (tentative title). Manuscript in prep.

Steffenrem A, Kvaalen H, Høibø OA, Bjoner S, Johnsen Ø, Skrøppa T. Genetic variation in wood density and relationships with bud phenology of *Picea abies* (tentative title). Manuscript in prep.

Steffenrem A, Kvaalen H, Høibø OA, Dalen K. A method for rapid determination of wood density within annual growth rings using x-ray computer tomography (tentative title). Research note in prep.

Ward EJ, Oren R, Sigurdsson BD, Jarvis PG, Linder S (2008). Fertilization effects on mean stomatal conductance are mediated through changes in the hydraulic attributes of mature Norway spruce trees. Tree Physiol. 28: 579–596.

2. Articles in international scientific compilation works and international scientific conference proceedings with peer review

Korpela M, Mäkinen H, Sulkava, M, Nöjd P, Hollmén J (2008). Smoothed prediction of the onset of tree stem radius increase based on temperature patterns. In: Boulicaut J-F, Berthold MR, Horváth T (Eds.). Discovery Science, 11th International Confernce, DS 2008, Budapest, Hungary, October 13-16, 2008, Proceedings, pp. 100-111.

Sulkava M, Mäkinen H, Nöjd P, Hollmén J (2008). Automatic detection of onset and cessation of tree stem radius increase using dendrometer data and CUSUM charts. In: Lendasse A (Ed.), European Symposium on Time Series Prediction, Otamedia, Espoo, Finland. pp. 77 - 86.

3. Articles in national scientific journals with peer review

4. Articles in national scientific compilation works and national scientific conference proceedings with peer review

Bergh J, Linder S (2010). Skogsbruket måste påbörja omställningen. In: Johansson B (Ed.) *Sverige i nytt klimat – våtvarm utmaning,* pp. 185-202. *Forskningsrådet Formas*. ISBN 978-91-540-6040-5.

Börjesson P, Linder S, Lundmark T (2008). Biomass in Sweden – a vast but still insufficient resource. In: *Bioenergy - for what and how much?* Johansson B (Ed.), pp. 69-85. *Forskningsrådet Formas*. ISBN 978-91-540-6006-1 (Also available in Swedish and Russian)

Linder S, Bergh J, Lundmark T (2008). Fertilization for more raw material from the forest! In: *Bioenergy - for what and how much?* Johansson B (Ed), pp. 215-227. *Forskningsrådet Formas*. ISBN 978-91-540-6006-1 (Also available in Swedish and Russian)

5. Scientific monographs

6. Other scientific publications, such as articles in scientific non-refereed journals and publications in university and institute series

Repo T, Manner M, Jyske T, Nöjd P, Mäkinen H (2009). Roudan vaikutus kuusen fenologiaan [Effect of soil frost on phenology of Norway spruce]. (in Finnish) In: Ruotsalainen S, Häggman J (Eds.). Risto Sarvas 100-anniversary book, Finnish Forest Research Institute, p. 99-105

Schiestl-Aalto P (2009). Männyn kasvun ja hiilenkäytön ajoittuminen vuoden aikana. [Timing of growth and carbon utilisation in Scots pine during the growing season]. (in Finnish) MSc Thesis. Department of Forest Ecology, University of Helsinki. 53 pp.

a) Other dissemination

Mäkinen H, Mäkipää R (2009). Mikä on hiilen kohtalo puun hajoamisprosessissa? [What happens to carbon during decay process?] Metsäntutkimus 1/2009: 29.

Mäkinen H, Jyske T, Nöjd P (2010). Kuivuus hidastaa kuusen kasvua [Drought decreases growth of Norway spruce]. Newsletter of the research programme “Functioning of forest ecosystems and use of forest resources in changing climate (MIL)” 2/2010. Finnish Forest Research Institute.

1.6 National and international cooperation

The project has ongoing close cooperation with with the Federal Research Centre for Forestry and Forest Products, Institute for Wood Biology and Wood Production (Hamburg, Germany), the VN Sukachev Institute of Forest (Siberian Branch, Russian Academy of Science) and INRA (Nancy, France) in sampling, measurements and developing methods for monitoring the rate of wood formation.

The collaboration with the Hawkesbury Forest Experiment in Australia, on the effects of drought and elevated atmospheric CO_2 concentration on physiology and growth of *Eucalyptus saligna*, has continued. The first experiment was harvested in March 2009 and wood samples were taken for later analyses. A pulse-labelling with C-13 was performed before harvesting the trees.

The project is in close contact with the SNS-network GENECAR (http://www.nordicgenecar.org/) and the EU-project TREEBREDEX (http://treebreedex.eu/) through Øystein Johnsen (NFLI), who is the coordinator of GENECAR and activity coordinator in TREEBREEDEX.

The project is in collaboration with the University of Edinburgh (Mauritzio Mencuccini) in developing the description of linkages between the sap transport, wood structure, and cambial growth and the signature of stable isotopes in wood growth. There is close contact in data production and collection with the Finnish Academy Centre of Excellence "Physics, Chemistry, Biology and Meteorology of Atmospheric Composition and Climate Change" and through the connection with EU FP6 IMECC project and international Fluxnet flux-measuring network.

The project is in close collaboration with the Forestry and Forest Products Research Institute (FFPRI) in Japan (Hisashi Abe), through Tuula Jyske (Metla), who worked at FFPRI as post-doctoral fellow in 2010. The timing and rate of cambial activity during the growing season was studied in clone trees of *Cryptomeria japonica*. Moreover, the day-length control of cambial activity and tree physiology (i.e., photosynthesis rate and tree water potential) of *Cryptomeria japonica* -seedlings was studied in growth chambers.