Dissertationes Forestales 138

Estimating forest growth and carbon balance based on climate-sensitive forest growth model and remote sensing data

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Academic dissertation

To be presented, with the permission of the Faculty of Science and Forestry of the University of Eastern Finland, for public examination in the auditorium F100 of the University of Eastern Finland, Yliopistokatu 7, Joensuu, on 20th January 2012, at 12 o'clock noon.

Title of dissertation: Estimating forest growth and carbon balance based on climate-sensitive forest growth model and remote sensing data

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Dissertationes Forestales 138

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ISSN 1795-7389
ISBN 978-951-651-366-2 (PDF)

(2012)

Publishers:
The Finnish Society of Forest Science
Finnish Forest Research Institute
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial Office:
The Finnish Society of Forest Science
P.O. Box 18, FI-01301 Vantaa, Finland
http://www.metla.fi/dissertationes

Härkönen, S. 2012. Estimating forest growth and carbon balance based on climate-sensitive forest growth model and remote sensing data. Dissertationes Forestales 138. 56 p. Available at http://www.metla.fi/dissertationes/df138.htm

ABSTRACT

A climate-sensitive process-based summary model was used to estimate forest growth and carbon balance with field inventory and airborne laser scanning data, which are easily available for practical forest planning purposes. The generalisation of forest carbon balance estimations for large areas was examined by using a *k* nearest neighbour imputation with Landsat satellite images. The estimations were evaluated using several data sets mainly provided by the National Forest Inventory of Finland. Also, the most common empirical forest growth models used in Finland were evaluated and compared against the process-based approach.

Reliability of the empirical and process-based summary models was at a similar level in the short run. In longer simulations, the role of mortality and regeneration models becomes increasingly important, so these models require special attention and further developing efforts in both approaches. In warming climate conditions or when testing new kind of management regimes, process-based approaches or hybrid models would be the most reasonable solution. However, further testing of the approach is required for a wider range of site types, tree species, mixed forests, geographical areas, as well as longer simulation periods, in order to draw conclusions of their reliability in larger scale use. There are also several development needs in the tested approach, such as adding nitrogen and water uptake processes to the simulator, linking it with mortality and regeneration models, as well as parameterising the model to peat lands.

The developed approach can be expanded to estimating carbon fluxes for large areas with LiDAR data. It could be linked with forest planning frameworks, which would accommodate for carbon balance issues in practical planning and optimisation tasks. The approach contains building blocks for developing a visual tool for examining the effects of forest management in changing environmental and climatic conditions for decision making, research, and policy making purposes.

Keywords: empirical growth models; process-based growth models; National Forest Inventory; LiDAR; satellite images; *k* nearest neighbour imputation

ACKNOWLEDGEMENTS

This PhD thesis is a result of research cooperation with numerous great colleagues working in fields of forest ecology, forest information systems and remote sensing both in Finland and abroad. First of all, I want to express my warmest thanks to my supervisors Prof. Timo Tokola and Prof. Annikki Mäkelä for their valuable advices, encouragement and support during this project. Thank you for giving me a chance to work with such an interesting mixture of different scientific worlds!

I want to express my gratitude to my co-authors Antti Mäkinen, Jussi Rasinmäki and Jouni Kalliovirta from Simosol Oy, Minna Pulkkinen from University of Helsinki, Remko Duursma from University of Western Sydney, Jari Vauhkonen and Petteri Packalén from the University of Eastern Finland, and Aleksi Lehtonen, Kalle Eerikäinen and Mikko Peltoniemi from the Finnish Forest Research Institute. Thank you for joining this work and sharing your knowledge on different forest-related issues. I am very grateful to the pre-examiners Dr. Risto Ojansuu and Dr. Harry Valentine, who both gave invaluable comments and advices related to this thesis.

My current and previous colleagues at the Finnish Forest Research Institute, University of Eastern Finland, University of Helsinki, and elsewhere, deserve big thanks for good cooperation. Special thanks go to Prof. Paavo Pelkonen and Dr. Petteri Vanninen, who were among the first persons who encouraged me to start PhD studies. Equally, I want to thank Dr. Raisa Mäkipää and her research team for providing inspiring and supportive atmosphere, which enabled this PhD effort to be finalised. Mirja, Katri, and other “forester ladies”: special thanks for good company both at work and in hobbies!

Finally, my dearest thanks go to my family, relatives and friends: thank you for standing always by my side! Anne, you deserve special thanks - your friendship and support has been irreplaceable. Tero, my loved one, thank you for giving me inspiration and for being there for me.

Joensuu, November 2011

Sanna Härkönen

LIST OF ORIGINAL ARTICLES

This thesis consists of this summary and the following studies, referred to in the text by their Roman numerals I-IV:

I **Härkönen, S.**, Mäkinen, A., Tokola, T., Rasinmäki, J., Kalliovirta, J. 2010. Evaluation of forest growth simulators with NFI permanent sample plot data from Finland. Forest Ecology and Management 259: 573-582.
doi:10.1016/j.foreco.2009.11.015

II **Härkönen, S.**, Pulkkinen, M., Duursma, R., Mäkelä, A. 2010. Estimating annual GPP, NPP and stem growth in Finland using summary models. Forest Ecology and Management 259: 524-533.
doi:10.1016/j.foreco.2009.11.009

III **Härkönen, S.**, Tokola, T., Vauhkonen, J., Packalén, P., Mäkelä, A. 2011. Linking airborne LiDAR data to a climate-sensitive forest growth model. Manuscript.

IV **Härkönen, S.**, Lehtonen, A., Eerikäinen, K., Peltoniemi, M., Mäkelä, A. 2011. Estimating carbon fluxes for large regions in Finland based on process-based modeling, NFI data and Landsat satellite images. Forest Ecology and Management 262: 2364-2377.
doi:10.1016/j.foreco.2011.08.035

Articles I, II and IV are reproduced with the kind permission from the publishers, while study III is the author version of the submitted manuscript.

Author's contribution

S. Härkönen is a corresponding author in all four papers and fully responsible for the data analysis and writing of this thesis.

Professor T. Tokola (studies I and III) and Professor A. Mäkelä (studies II-IV) participated in planning of the studies as supervisors. **In study I**, A. Mäkinen, J. Rasinmäki and J. Kalliovirta provided the simulation chains in SIMO framework and helped to modify them for this study. **In study II,** M. Pulkkinen and R. Duursma helped with modeling issues. **In study III** J. Vauhkonen and P. Packalén helped with calculating the LiDAR metrics. **In study IV** A. Lehtonen and M. Peltoniemi participated in planning of the study, and K. Eerikäinen calculated tree-wise estimates of tree and crown base heights based on the NFI data and wrote about field data processing.

All the persons mentioned above participated the writing process by providing information and giving comments on the manuscripts.

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1 INTRODUCTION

Forest growth simulators allow the rapid prediction of the potential growth of a forest and its response to management over a long time period, which makes them versatile tools in both practical forest planning and research, as well as for policy making purposes. Simulators are essential tools for examining and comparing the results of different treatment scenarios, and they are useful in determining optimal management solutions (for example, Hyytiäinen et al. 2006, Hynynen et al. 2005). Forest growth simulators have a long development history, but their use still has several drawbacks. The problems are partly related to insufficient or biased input data, typically caused by inaccurate inventory methods, but also the forest growth prediction procedure itself always contains errors, as the real-life phenomena affecting growth can never be included in the models with sufficient detail (Schmidt et al. 2006). Therefore, the reliability of forest growth models in predicting growth varies depending on, for example, forest structure, age, region, tree species, and soil type (Hynynen et al. 2002). Especially, regeneration dynamics (Miina et al. 2006), development of young stands (Huuskonen and Miina, 2007), development of uneven-aged forests (Pukkala et al. 2009), and tree mortality (Aakala et al. 2009) are episodic phenomena, and thus problematic to model. Also, growth estimates for peat land stands are often less reliable than those for mineral soil stands (Hynynen et al. 2002), due to higher variation in water and nutrient balance in drained peat lands (Jutras et al. 2003).

Forest growth models can be classified into empirical models, which rely on forest development data measured in the past (for example, Hynynen et al. 2002), and to process-based models, which predict the forest growth based on tree vital functions and prevailing weather conditions (Kortzhukin et al. 1996, Mäkelä et al. 2000). A third category, a mix between these two, includes hybrid models (Mäkelä et al. 2000), which are combinations of empirical and process-based models still functioning with a realistic amount of input data, but being flexible under changing environmental conditions (for example, Landsberg 2003, Valentine and Mäkelä 2005, Peng et al. 2002). Hybrid approaches have been applied in Finland to estimate forest growth response in elevated temperature and CO_2 concentration conditions, for example, in studies by Nuutinen et al. (2006) and Matala et al. (2006), where the core of the simulator was based on the empirical models of Hynynen et al. (2002); the physiological effects were taken into account by calculating transfer functions based on the process-based FinnFor model (Kellomäki and Väisänen 1997).

Summary models are simplified versions of detailed process models, which are potentially applicable to practical forestry. For instance, the 3-PG model by Landsberg and Waring (1997), a simplification of the FOREST-BGC model by Running (1994), has been applied to practical forest management in different tropical countries (Almeida et al. 2010). Summary models are advantageous, because they are based on tree physiology and climate input, the model structure remains clear and the required input data as well as the number of parameters are at a realistic level. In addition to parametric models, growth can be estimated using non-parametric methods, such as the *k* nearest neighbour imputation (k-NN) (Sironen 2009), which has been found to be a successful approach for reducing regional biases and for extending the plot wise estimations to the regional level (Tomppo 1990, Korhonen and Kangas 1997).

Until now, the empirical growth models have been the most common model type in practical forestry, as they are considered to be the most accurate ones and the required input data has been available from basic field inventories. The most popular models used in practical forestry in Europe are empirical tree-level models, obviously due to their capability to estimate growth even in heterogeneous stands (Mäkinen et al. 2008). In Finland, the most commonly used empirical tree-level models are those of Hynynen et al. (2002), which are included in the practical forest planning simulators, such as the MELA (Siitonen et al. 1996), SIMO (Tokola et al. 2006, Rasinmäki et al. 2009), and MOTTI (Hynynen et al. 2005) frameworks. European examples of tree level empirical simulators include SILVA developed in Germany (Pretzsch et al. 2002), the Austrian PrognAus (Ledermann, 2006), and the Slovakian SIBYLA (Fabrika and Ïurský, 2006). In practical forestry, however, usually only stand level inventory data is available, which means that with tree-level models the data must first be down-scaled from the stand level with distribution models. Another model type, stand-level models, would be directly applicable to the stand-level inventory data, but as these models ignore variation inside the stand, they cannot be properly used for uneven-aged or mixed stands. This is one of the reasons for replacing them by tree-level models in many cases (Garcia, 2001, and Porté and Bartelink, 2002). However, the stand-level models have been successfully utilized in many applications, especially in long-term simulations (Vanclay, 1995, Atta-Boateng and Moser, 2000, and Garcia, 2001). Examples of empirical stand-level models applicable in Finland include models by Vuokila and Väliaho (1980) for conifers, and the birch models of Mielikäinen (1985), Oikarinen (1983), and Saramäki (1977).

The ability to adapt to changes in our environment and climate is one of the main challenges in developing reliable forest growth models. Current changes in the climate as well as the demand for multiple use of forests create additional challenges for growth simulators. Forest management regimes and softer forest treatments are needed especially in areas that are near cities, tourist resorts, or nature conservation areas. Public interest in utilizing tree biomass as bioenergy and managing forests as carbon sinks also has grown stronger. This means that one should be able to include new kind of optimization goals (biodiversity, recreational use, scenery, carbon sequestration etc.) in the simulating routines. Most of the current forest planning softwares use empirical models to predict growth. These work well while the climatic conditions and management practices stay similar as in the past, but when the climate or management changes, the models may become less reliable. In this situation, weather-driven process-based forest growth models offer a relevant tool for estimating forest growth, in contrast to traditional empirical growth models which rely on data measured in the past. Because process-based models are able to produce carbon flux estimates, such as gross primary production (GPP), net primary production (NPP), and the whole net ecosystem exchange (NEE), they can be utilized for defining topical issues, such as which kind of forests tend to be carbon sinks or carbon sources, and how the carbon balance changes when either climate or forest management regimes change.

Process-based models have not been common tools in practical forestry, since they have been found too complex to use and difficult to parameterize (Mäkelä et al. 2000, Peng et al. 2002, Matala et al. 2006). The key input variables in the photosynthesis driven models are related to crown leaf biomass and crown structure, and since these variables are difficult and too laborious to accurately measure in a traditional forestry field inventory, they have typically been produced using allometric equations derived from basic field measurements. However, recent efforts in developing summarized versions of process-based models and increasing availability of relevant input data derived from remote sensing products can offer a solution to the problem (Landsberg and Waring, 1997, Mäkelä et al. 2000, Study II) and make process-based models applicable to practical forestry.

Remote sensing products can be utilized for complementing or producing the input variables required in the process-based models (Turner et al. 2004), as tested with the 3-PGS model based on satellite images by Coops et al. (2007) and Nole et al. (2009). Satellite images can also be used for estimating leaf area index (Stenberg et al. 2008), and mean tree size (Woodcock et al. 1994). Other examples of remote sensing products applicable to process-based models include high resolution AVIRIS images, which have been used for estimating canopy nitrogen (Smith et al 2002), and a synthetic aperture radar (SAR) for estimating vegetation biomasses (Saatchi and Moghaddam 2000). An especially interesting data source is airborne light detection and ranging (LiDAR), which has become commonly available for forest management purposes in recent years, at least in Scandinavia. LiDAR provides information on the forest crown structure and other relevant input data for growth models (Næsset and Okland 2002, Lim et al. 2003, Waring et al. 2009). Thus far, LiDAR data has been used for estimating several ecological variables, such as leaf area index or light interception (for example, Lefsky et al. 1999, Lefsky et al. 2002, van Aardt et al. 2008, Lee et al. 2009). However, there have been only a few studies utilising LiDAR with process-based models in the whole growth estimation chain (for example, Taguchi et al. 2007, Kotchenova et al. 2004).

At present, applying a simplified process-based growth model to produce traditional and carbon flux estimates over large areas has become possible in Finland, owing to the availability of the required up-to-date input data from a sample plot network covering the whole country (weather data from the Finnish Meteorological Institute and NFI data from the Finnish Forest Research Institute). By producing the desired estimates for the sample plot network and generalizing them based on satellite images, it is possible to impute the estimates for all the forested areas in the country. This kind of methodology has been applied to, for example, a multi-source forest inventory to produce estimates for stand characteristics (Tomppo 1990, Tomppo et al. 2008), forest biomasses (Labrecque et al. 2006, Muukkonen and Heiskanen 2007, Tuominen et al. 2010), and forest carbon pools (Dong et al. 2003, Stumer et al. 2010).

Objectives

The main goal of this study is to evaluate a climate-sensitive process-based summary model approach for estimating forest growth and carbon fluxes in the Finnish conditions, using input data that is also available for practical management purposes. Further, the applicability of the approach with remote sensing products, such as LiDAR data and satellite images, is examined. In addition, the reliability of the currently used empirical tree and stand-level simulators is examined. The interactions of the data and models applied in studies I-IV are visualized in Fig. 1.

The reliability and accuracy of the process-based approach is examined by comparing the simulated results with those obtained by empirical tree-level simulators and field observations. Further, the complementation of the process-based simulation approach with remote sensing data is investigated in two cases: 1) the input data for the process-based summary model is obtained purely from LiDAR measurements, and 2) satellite images are utilized for up-scaling the plot level results to regional level with the k-NN imputation. The objectives of this thesis include the following:

- **Evaluation of the traditional Finnish empirical forest growth simulators** constructed with the SIMO framework using 1) tree-level models (Hynynen et al. 2002), 2) stand-level models (Vuokila and Väliaho, 1980; Mielikäinen, 1985; Oikarinen, 1983; Saramäki 1977), and 3) combinations thereof with the Finnish National Forest Inventory (NFI) permanent sample data (from 1985 and 1995) in Southern Finland (Study I).

- **Development and evaluation of a climate-sensitive process-based summary model approach for estimating forest growth** by combining existing models: pipe theory (Shinozaki 1964a, Shinozaki 1964b, Mäkelä 1997, Ilomäki et al. 2003, Kantola and Mäkelä 2006), a light use efficiency model (Mäkelä et al. 2008b), and effective extinction coefficient (Duursma and Mäkelä 2007) (Study II). Complementing the approach with a dynamic bridging model by Valentine and Mäkelä (2005) with capability capable to estimate the development of both traditional stand characteristics and carbon balance, and assessing its reliability (Study III). Testing the approach for estimating carbon fluxes (GPP, NPP and NEE) for NFI data set by complementing the simulator with the Yasso07 soil carbon model (Tuomi et al. 2008) (Study IV).

- **Investigation of the applicability of remote sensing data with the process-based approach** by examining the applicability of LiDAR data as an input for the dynamic model (Study III) and assessing the use of Landsat TM 5 images with k-NN imputations for generalizing the carbon flux estimations for large regions, and comparison of the results with Eddy flux measurements from Sodankylä and Hyytiälä (Study IV).

2 MATERIAL

2.1 Field sample plots

Finnish National Forest Inventory data (NFI) established by the Finnish Forest Research Institute was utilised in studies I, II, and IV, while in Study III, the field data came from forest inventory conducted by the University of Eastern Finland in the Heinävesi (Matalansalo) region (Fig. 2). The mean stand characteristics are presented in Table 1. For the stand-level models (empirical model in Study I, process-based model in studies II-IV), the tree data was first aggregated to stand level. The field data was used both as input for the models and for comparing reliability of the simulators. Details of the Finnish NFI, which has fairly similar history and principles as, for example, the Swedish NFI (Tokola 2006), can be found in Tomppo (2006).

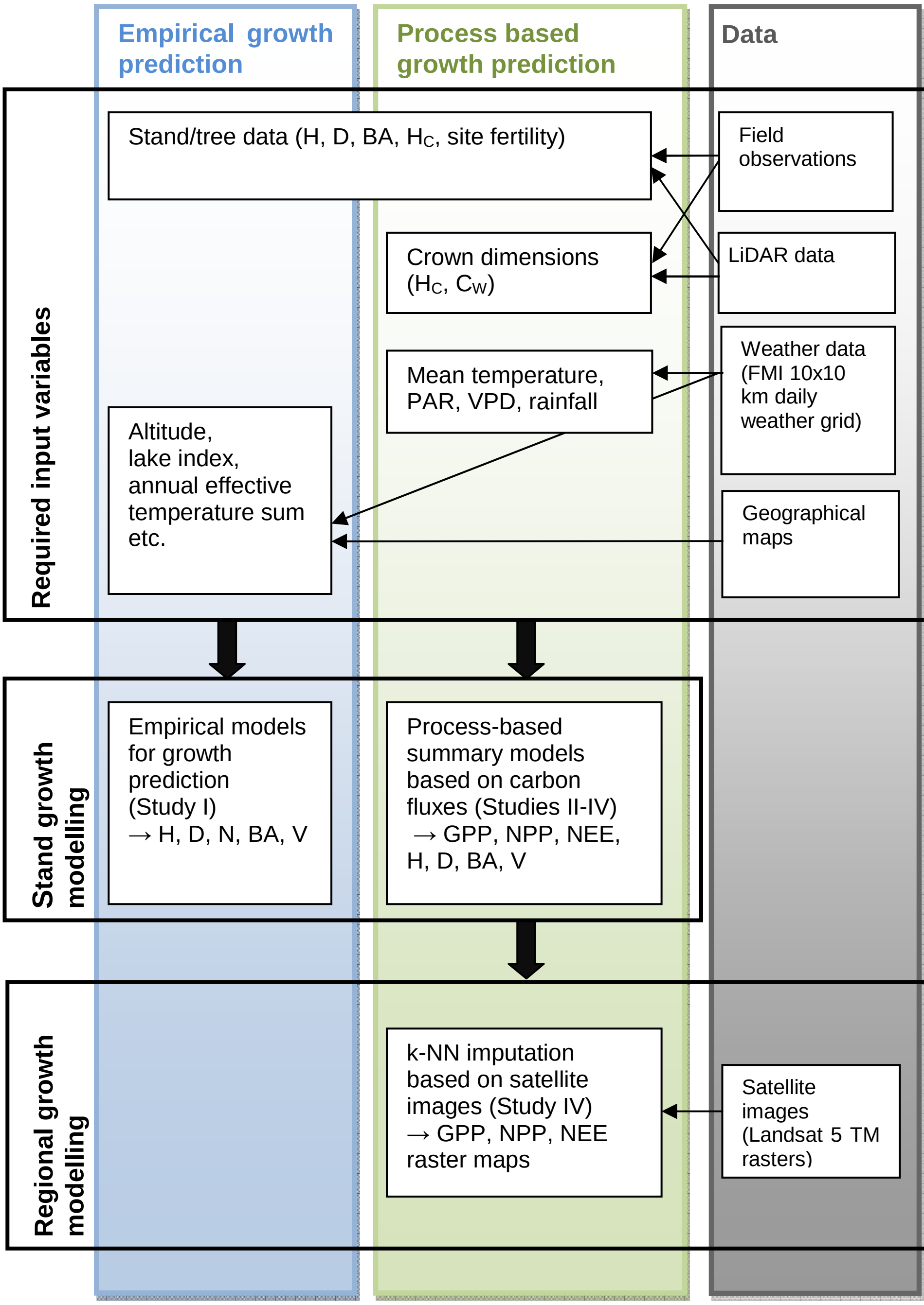

Figure 1. Framework of the data and growth estimation procedures applied in the studies I-IV.

In Study I, the main material was based on the permanent NFI sample plots located in Southern Finland and established by the Finnish Forest Research Institute (Fig 2., Table 1). The NFI sample plot network was based on systematic sampling of field tracts, where each tract in Southern Finland included four plots located 400 metres apart (from north to south), the tracts themselves being 16 km apart (from north to south, and from east to west). The plot size varied according to the tree diameter at breast height, being 100 m^2 when the diameter was under 10.5 cm, and otherwise 300 m^2. The trees with diameter smaller than 4.5 cm were measured only if they were considered to survive alive until the next measuring round. The decision was done based on the tree species, site type, regeneration type and tree position. All the Southern Finland NFI plots (below latitude of around 65°) measured both in 1985 and in 1995 were included, with the exception of plots located on waste or scrub land, plots which consisted of two or more stands either in 1985 or in 1995, plots where there had been cutting during the simulation period, and some plots with easily detectable coding errors, such as a large number of missing trees according to the data without cutting. Also, all dead trees were excluded. Data measured in 1990 was also utilised, because it contained information about the thinnings between 1985-1990. A total of 597 sample plots were included in the study (the original Study I had 837 sample plots, but recently it turned out that some of them had been subject to thinning in 1985-1990. The results presented in this summary have been calculated using only the unthinned plots (n=597). The NFI material contained the following tree data: diameters at breast height for all the trees and heights for the sample trees, from which mean and total values per hectare were aggregated for each plot. The tree volumes were estimated using volume functions of Laasasenaho (1982) based on the tree diameter and height. Tree heights for the non-sample trees were estimated from tree diameter and other stand data using the tree height models of Veltheim (1987). Models for Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) and silver birch (*Betula pendula* Roth., applied to all deciduous trees) were used. The modelled heights were scaled to follow the level of the sample tree heights by multiplying the modelled heights by the stand-wise ratio of the measured to modelled mean height of the sample trees. The reference data for 1995 contained only the trees that already existed in 1985 and were still alive in 1995. The trees were identified by measuring their distance and angle from the sample plot identification point. Scots pine was the main tree species (in terms of basal area) on 54.1% of the plots (n=597), Norway spruce on 36.7%, and birches on 8.9% of the plots.

In Study II, a subset of the same NFI data set used in Study I was utilised for testing the model (Fig 2, Table 1). A total of 137 sample plots were included in the analysis using the following criteria: (1) the sample plot was located on mineral soil, (2) it consisted of only one management unit, (3) the plot had not been subject to thinning, cuttings or mortality during the period from 1985 and 1995, (4) the plot data contained all the required sample tree measurements for the Scots pine, Norway spruce, and deciduous strata that existed in the plot, (5) the plot site type was *Oxalis-Myrtillus*, *Myrtillus*, *Vaccinium*, or *Calluna* (Cajander 1925), and (6) the plot data were free of obvious measuring/coding errors. All dead trees and trees born between 1985 and 1995 were excluded from the material. The stand-level mean and sum attributes were calculated similarly as in the Study I and using only those trees alive during both the 1st and the 2nd NFI rounds.

In Study III, data from Heinävesi (Matalansalo), Eastern Finland, around latitude 62° N, from 2004 and 2009 was used (Fig 2, Table 1). A total of 52 sample plots were included in the analysis, selected with criteria that the main tree species in the plot was Scots pine (> 75% of the basal area). The sample plots were circular plots with a radius of 9 m. Diameter and tree species were collected of all the trees in the plot (tally trees), and tree height and crown base height were measured for the sample trees (crown base was measured only in 2009). The drilled growth samples (5 years growth in radius at 1.3 m height) taken from all the sample trees representing the dominant layer in 2009 were used for generalising the basal area growth for all the tally trees from 2004, which is presented in detail in Study III. Using the growth samples was assumed to produce more reliable ground truth values for basal area growth, than using simply the increment in the field measured basal area, because the inventories in 2004 and 2009 were not conducted in the same time during the growing season. Therefore, the field-observed difference in the basal area between the years 2004 and 2009 would have not actually represented the full 5-year growth. In addition, some of the tally trees might have died or fallen down since 2004, and there might have been also slight differences in the sample plot locations between the years 2004 and 2009 due to GPS.

In Study IV, the field data was retrieved from the Finnish National Forest Inventory (NFI) data from Central Finland and Lapland from 2004-2008 (Fig 2., Table 1). A total of 1072 sample plots from Central Finland and 365 plots from Lapland were included in the analysis, selected with criteria that the whole plot consisted of only one stand, the plot was on mineral soil, and the plot was located in the selected Landsat images. The sample plots were circular plots with maximum radius of 12.52 m in Southern Finland (Central Finland data) and 12.45 in Northern Finland (Lapland data). The tally trees were selected with a relascope coefficient of 2 in Southern Finland and 1.5 in Lapland. Every 7th tree over the whole inventory area was measured as a sample tree. Tree diameter and tree species were collected of the tally trees and tree height and crown base height were measured only for the sample trees. The heights and crown base heights for the rest of the trees were estimated using models of Eerikäinen (2009).

Table 1. Mean stand characteristics of the sample plots included in the analysis.

	NFI permanent plots, 1985 and 1995 (Study I) [8)]	**NFI permanent plots, 1985 (Study II)**	**Sample plots Matalansalo, 2004 (Study III)**	**NFI plots, 2004-2009 (Study IV)**
Mean tree height, basal area weighted (m)	12.4[2)], 14.8[3)]	12.6[4)], 13.6[5)], 11.5[6)]	16.4	15.7[7)], 11.8[8)]
Mean tree diameter, basal area weighted (cm)	16.7[2)], 19.3[3)]	17.5[4)], 18.3[5)], 4.6[6)]	19.2	20.3[7)], 19.3[8)]
Mean stand basal area ($m^2 ha^{-1}$)	16.4[2)], 21.6[3)]	-	21.6	18.7[7)], 11.9[8)]
Mean number of trees per hectare	1398[2)], 1312[3)]	1071	1270	-
Number of sample plots	597	137	52	1072[7)], 365[8)]
Share of peat lands (%)	24.8	0	0	0

[1)] Contains only the un-thinned plots used in the summary of the thesis, selected out of the plots in the original Study I [2)] NFI 1985, [3)] NFI 1995, [4)]Scots pine strata, [5)] Norway spruce strata, [6)] deciduous strata, [7)] Central-Finland plots, [8)] Lapland plots

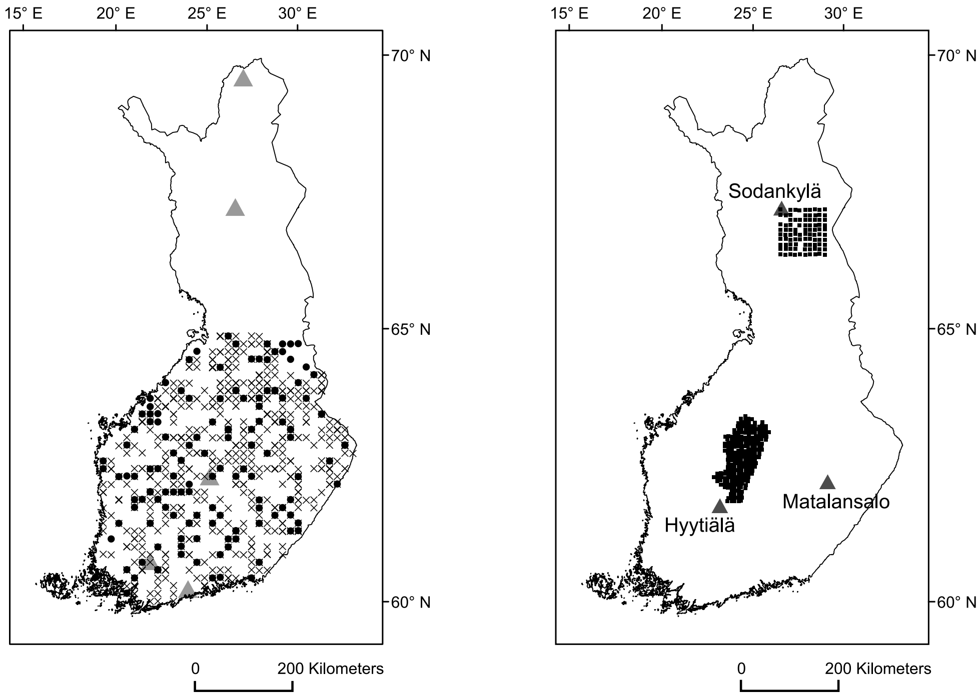

Figure 2. Left: Location of the NFI sites included in Study I (crosses + black dots), in Study II (black dots), and the weather stations used in Study I (grey triangles). **Right:** Location of the Matalansalo Study area (Study III) and the NFI sites (black dots) and eddy flux sites in Sodankylä and Hyytiälä included in Study IV.

2.2 Remote sensing data

LiDAR data

The laser scanning data used in Study III was gathered at night on 4 August 2004 using Optech ALTM 2033 laser scanning system at an altitude of 1,500 m above ground level with a half angle of 15° from Heinävesi (Matalansalo), Eastern Finland. The width of each laser strip was 800 m and the pulse density was 0.7 pulses per m^2. The footprint was 45 cm. All together seven strips were scanned with a 35% overlap, yielding about 20 km^2 in total area.

Landsat TM 5 Satellite Images

In Study IV, two study areas, covering parts of Forest Centres of Central Finland and Lapland provinces, were selected for the analysis. Landsat 5 TM images from 2007 and a digital elevation model (DEM) of the corresponding area were used as independent variables in the k-NN imputation. The image for the western part of Central Finland (path 190, row 16-17) was taken on 2.6.2007. For Lapland, two images taken on 2.6.2007 and 4.7.2007 (path 190, row 13) were used. Images were georeferenced to the Finnish uniform coordinate system. The resolution of the Central Finland image was re-sampled to 25 m. For Lapland, the resolution was 30 m. Georeferencing and re-sampling were carried out using the ArcGIS 9.3 software.

2.3 Weather data

The weather data used in the process-based model (Studies II-IV) was received from the Finnish Meterorological Institute (FMI), and it consisted of daily measurements of global radiation (W m^{-2}), relative humidity (%), rainfall (mm), and temperature (°C) for all the years between 1961 and 2008, in the form of a 10 km x 10 km grid across Finland (Venäläinen et al. 2005).

2.4 Data from Eddy flux sites

Eddy covariance data containing GPP and NEE data for 2004-2008 from Hyytiälä (61°50’N, 24°17’E) and Sodankylä (67°21’, 26°38’) (Fig. 2) were used for examining the accuracy of simulations and imputations in Study IV. The eddy flux measurements were compared with 1) the average of imputed pixel values around the eddy towers within a circle of radius of 100 m, and 2) GPP and NEE values obtained by simulating forest growth with the stand input data from the eddy flux sites. In the latter case, the simulations in Hyytiälä were conducted for all the years between 2004 and 2008 with the site and weather data from the corresponding years. In contrast, for Sodankylä site data was only available from 2000, which was then used as the input in all the simulations meaning that only the weather data varied (2004-2008). The Hyytiälä data was from measurements by University of Helsinki (Dr. Pasi Kolari), see Ilvesniemi et al. (2009) for description of the field measurements. The Sodankylä data was from measurements by the Finnish Meteorological Institute (Dr. Mika Aurela).

3 METHODS

3.1 Empirical growth models

For Study I, three alternative simulators based on empirical models were constructed in the SIMO simulation framework, which offers an open source platform for building simulation chains: 1) a tree-level simulator based on tree-level growth models, 2) a stand-level simulator based on stand-level growth models, and 3) a combined simulator, where the first 5 years are simulated using tree-level models and the remaining years using stand-level models. The growth models were run with 5 years' time step, but the simulator reported annually the stand- and stratum level mean diameters, mean heights, basal areas, and volumes, based on average annual growth in 5 years.

In Study I, the growth and yield models used in the tree-level simulator were those of Hynynen et al. (2002), which are also used in the MELA simulator. These included individual growth models for estimating the growth of tree height and basal area of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), silver birch (*Betula pendula*), and white birch (*Betula pubescens*). Models for self-thinning and mortality were used, but the ingrowth model was not applied to these simulations. The trees measured in the field were used to construct tree lists for the simulator. The input variables included e.g. tree diameters for all the tally trees and heights for the sample trees, number of trees per hectare represented by each tree, stand coordinates and site type. Crown base heights were estimated using a crown ratio model by Hynynen et al. (2002). Several new variables were calculated further by the simulator, such as dominant diameter of the stand, growth in dominant height, crown ratio, dominant growth ratio, relative density factor, and site index. These were used as independent variables in the growth models, where the dependent variables were increment of tree height and basal area. Stand volumes were estimated using the volume equations of Laasasenaho (1982). The same empirical tree-level models were used also in studies II and III for comparing with the process-based model results, but without the mortality and self-thinning models.

The stand-level growth models for pine and spruce used in study I were those of Vuokila and Väliaho (1980) and the growth models for birches those of Mielikäinen (1985), Oikarinen (1983), and Saramäki (1977). These included a number of individual regional models, as growth conditions vary across Finland. The independent variables of the stand-level models included e.g. stand basal area, stand age, dominant height and site index. These were calculated based on the input variables of the simulator, which included e.g. tree diameters for all the tally trees, heights for the sample trees, number of trees per hectare represented by each tree, stand age, stand coordinates and site type. Site index was determined based on site type. The dependent variables of the stand-level models included e.g. increment in basal area, volume and dominant height. Other output variables were calculated based on model results, e.g. stand mean height was predicted from dominant height and stand mean diameter from mean height, mean age, temperature sum, and site class. The stand-level simulator does not include mortality models as such, but the growth models include the effect of tree removal, due to modelling data is from normally thinned forests.

3.2 Process-based summary model

In studies II-IV, the process-based model was used with different compositions. In the studies II and IV, a static version, later referred to as *static process-based model*, was applied to estimate one-year gross primary production (GPP), net primary production (NPP), and growth of stem biomass in the stand. In Study III, the static approach was complemented by a dynamic growth component based on the bridging model by Valentine and Mäkelä (2005), later referred to as *dynamic process-based model*, which is capable of simulating dynamic growth of the tree dimensions and development of the carbon balance over several years. In Study IV, the soil carbon model Yasso07 (Tuomi et al. 2008, Tuomi et al. 2009) was also applied with the static version to estimate net ecosystem exchange (NEE). The main principles of the approach are explained shortly below, and the framework of the model interactions is demonstrated in Fig. 3. The data used in developing of the above-mentioned models is fully independent from the test data used in the studies II-IV. A detailed explanation of the approach is provided in Appendix 1.

In the process-based summary approach, tree growth is estimated at stand level, based on carbon production and respiration in different components of trees. Annual forest growth P_N (kg C ha^{-1} yr^{-1}), i.e. NPP, can be expressed as

$$P_N = P - R_M - R_G, \tag{1}$$

where P is GPP, R_M is the maintenance respiration, and R_G is the growth respiration of the trees. NPP can also be expressed as $P_N = r_{NPP}\, P$, where r_{NPP} is the NPP:GPP ratio depending on the respective rates of maintenance and growth respiration of the stand. Annual biomass production G_t (kg DW ha^{-1} yr^{-1}) (DW=dry weight) is proportional to *NPP* as follows:

$$G_t = c_C^{-1} P_N\,, \tag{2}$$

where c_C is the carbon content of biomass dry weight ($c_C \approx 0.5$). *GPP* depends on environmental driving variables and forest stand data as follows:

$$P = f_{APAR}\, P_0, \tag{3}$$

where f_{APAR} is the (effective annual) mean fraction of photosynthetically active radiation (PAR) absorbed by the canopy, and P_0 (kg C ha^{-1} year^{-1}) is the annual canopy photosynthesis in a (hypothetical) canopy that absorbs all PAR radiation. This means that f_{APAR} represents the effect of forest structure on growth, while P_0 describes climatic effects. In studies II-IV, f_{APAR} was estimated using the Lambert-Beer formula based on effective extinction coefficient k_{eff}, as introduced by Duursma and Mäkelä (2007), and leaf area index (LAI). Effective extinction coefficient was calculated based on a homogenous extinction coefficient, K_H, crown surface area, S_A (m^2), and mean leaf area per tree, L_A (m^2). Leaf area index was derived from the leaf biomass, W_F (kg DW ha^{-1}), and the assumed specific leaf area (SLA, m^2 (kg DW)$^{-1}$) of the tree species (Luoma 1997). P_0 was estimated based on the LUE model (Monteith 1977, Mäkelä et al. 2008b). Biomasses for different tree components W_i (W_F=foliage, W_B=branches, W_S=stem, W_{CR}=coarse roots, and W_{FR}=fine roots) were estimated based on pipe-theory based equations for Scots pine (Mäkelä and Vanninen 2001, Vanninen and Mäkelä 2005), for Norways spruce (Kantola and Mäkelä 2006), and for birches (Ilomäki et al. 2003) (see Appendix 1, table A.2).

Net ecosystem exchange (*NEE*), E_N, can be derived from *NPP* (P_N) and heterotrophic respiration from the soil, R_H, as follows:

$$E_N = -(P_N - R_H). \tag{4}$$

R_H (Study IV) was estimated using the Yasso07 soil carbon model (Tuomi et al. 2008, Tuomi et al. 2009) based on litter fall data derived from biomass estimates (Liski et al. 2006). The growth of stem and crown dimensions (Study III) was estimated using the bridging approach introduced by Valentine and Mäkelä (2005), which is based on the pipe theory.

The static version of the process-based approach (Study II and IV) is applicable to Scots pine, Norway spruce, and deciduous stands, or a mixture thereof, in the Finnish conditions. The dynamic version used in Study III was applied to Scots pine stands only, but it could easily be extended to Norway spruce and birch.

3.3 Deriving stand characteristics from LiDAR data

In Study III, the process-based model was tested with input variables derived from LiDAR data. First, a digital terrain model (DTM) was generated from the LiDAR data as explained in Study III. The canopy height model was built using an interpolation procedure introduced in the Study by Packalen et al. (2008). The LiDAR based canopy height model was segmented into trees (or tree groups) using a watershed segmentation algorithm, which was then processed in an alpha shape program (Edelsbrunner and Mücke 1994; http://www.cgal.org). Estimates for plot wise mean height and total crown volume were obtained as an area weighted average of the height values and sum of the triangulation based volumes, respectively, of the segments located in the plot. Mean crown base height was also an area weighted average calculated from segments for which the crown base height values had been produced by the alpha shape approach (Vauhkonen 2010).

Several LiDAR metrics were calculated separately for the first (F) and last (L) returns. The number of trees per hectare, *N*, was estimated using the equation by Suvanto et al. (2005) fitted with the data from the same area as used in Study III. The mean tree crown volume was defined as the total crown volume divided by the estimated number of trees per plot, and it was used for determining the mean tree’s leaf biomass. Leaf biomass and crown dimension data of Scots pine measured in Southern Finland (Vanninen and Mäkelä 2000, Vanninen and Mäkelä 2005) were used for plotting an equation between tree crown volume and leaf biomass. The equation was used to convert the mean crown volume to mean leaf biomass per tree (see Study III for details). Further, the stand leaf biomass was determined as the mean tree’s leaf biomass multiplied by the number of trees per hectare estimated from LiDAR. The mean crown width was determined from the LiDAR based mean tree crown length and the estimated crown volume of the mean tree assuming the crowns as ellipsoids.

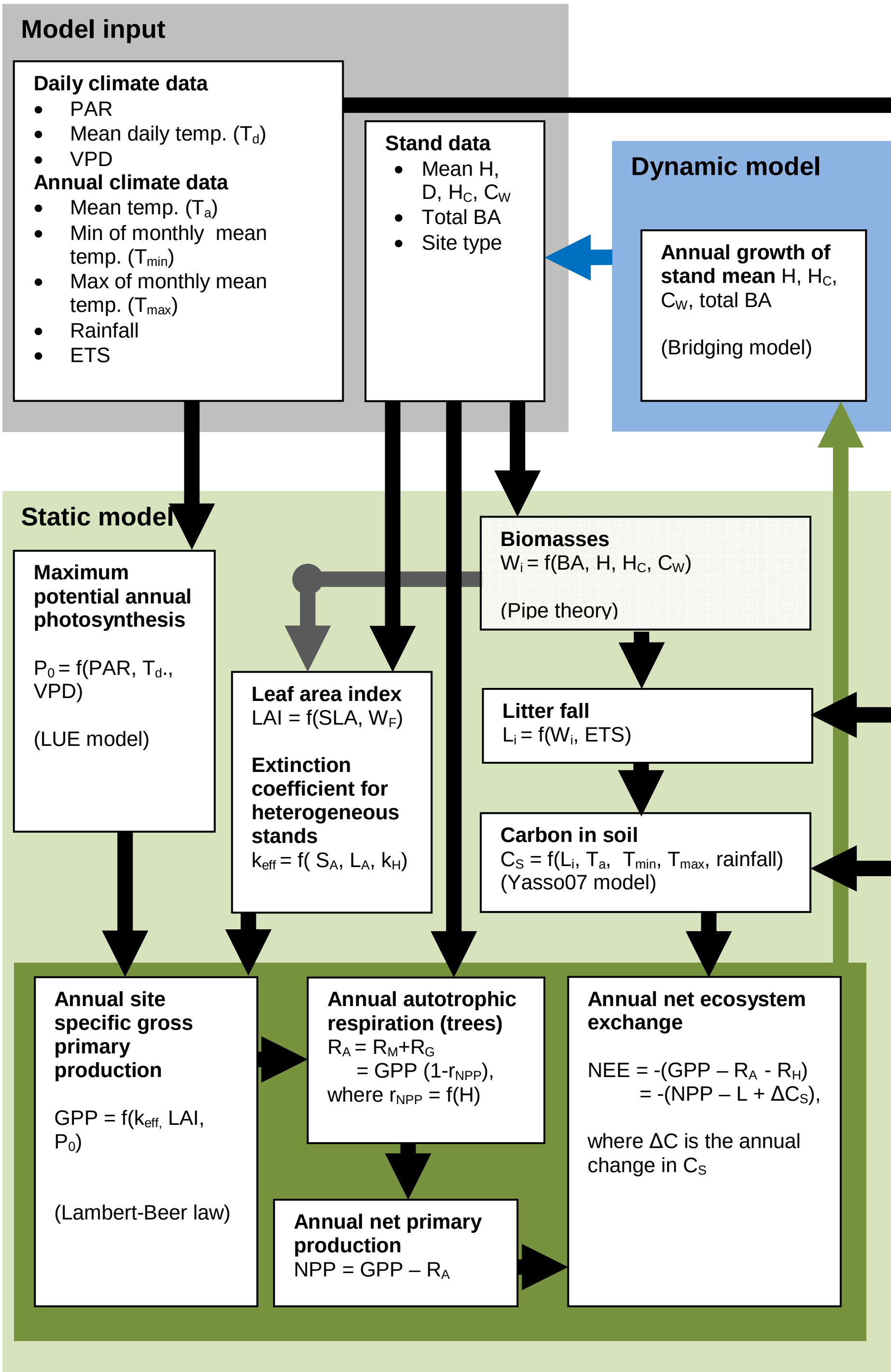

Figure 3. Description of the process-based approach. See Appendix 1 for the referred parameters and equations.

3.4 Generalisation of carbon flux estimates to regional level based on satellite images

In Study IV, the GPP, NPP, and NEE estimates for the years 2004-2008 were produced for the NFI sample plots in Central Finland and Lapland. The obtained results were then generalized for all the forested areas around the selected sample plots using the k-NN imputation based on Landsat 5 TM satellite images. In addition, the corresponding values were imputed for the Hyytiälä research area, located close to the Central Finland area, using the Central Finland training set.

Two different sets of independent variables were tested separately for the Central Finland and Lapland areas: 1) only channels 2-4 (green, red, and near infrared) as independent variables, and 2) all the channels (1-5, 7) as independent variables. Further, the usage of two images from the same growing season as well as of DEM as an independent variable were investigated in Lapland. The additional test runs for Lapland contained the following independent variables: 1) channels 2-4 from two different images, and 2) channels 2-4 from two different images and the digital elevation model. In Lapland, the imputations were tested with varying *k*'s (k=3, 5,..,11, 13); in contrast, in Central Finland *k*=5 was used. The nearest neighbours were defined using the Euclidian distance *d* as a measure, and the estimated *Y* value was defined as the distance weighted mean of the nearest neighbours' *Y* values, the weighting being $1/(1+d)$. The k-NN imputations were done using the yaImpute package in R Statistics (Crookston and Finley 2008).

3.5 Evaluation of estimates

In Study I, the reliability of the different empirical simulators (tree-level, stand-level, and combination thereof) was evaluated by examining their estimates of stand-level and stratum-level basal area weighted values of mean height, H (m), mean diameter, D (cm), stem volume, V (m^3 ha^{-1}), and basal area, BA (m^2 ha^{-1}), and comparing them with the field observations from NFI (1995).

In Study II, the reliability of the static process-based summary model was examined by comparing its estimates against the NFI field observations (1985-1995) and estimates obtained with the empirical tree-level model of Hynynen et al. (2002). The examined variables consisted of mean annual stand level stem biomass growth, $W_{S,G}$ (kg DW ha^{-1} $year^{-1}$), and stem volume growth, V_G (m^3 ha^{-1} $year^{-1}$).

In Study III, the reliability of the dynamic process-based summary model was investigated in two cases: 1) the input data was yielded by a traditional field inventory, and 2) the input data was from LiDAR. The examined variable was the total basal area after the 5-year growth period, which was compared with the basal area from the field observations (2004-2009) and the estimates obtained with the empirical tree-level model (Hynynen et al. 2002).

Table 2. Statistical equations used in the analysis. y_i is the reference value in a plot i, $\hat{y}_i$ is the estimated value in a plot i, $\bar{y}$ is the arithmetic average of the y values, and *n* is the total number of plots.

Statistics	Equation
Root mean squared error	$RMSE = \sqrt{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2 / n}$
Relative root mean squared error	$RMSE_{\%} = RMSE / \bar{y} \times 100$
Absolute bias	$BIAS = \sum_{i=1}^{n}(y_i - \hat{y}_i) / n$
Relative bias	$BIAS_{\%} = BIAS / \bar{y} \times 100$
Relative standard deviation of the estimation errors	$s\% = \sqrt{RMSE\%^2 - BIAS\%^2}$
Degree of determination	$R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2}$

In Study IV, the accuracy of the GPP, NPP, and NEE estimates based on k-NN imputations, obtained by the static process-based summary model and Landsat 5 TM satellite images, was investigated with a leave-one-out cross-validation. This was done by imputing new values for each reference data pixel (the NFI plot pixels) based on the rest of the reference data values. Reliability of the simulator itself was assessed by comparing the GPP (g C m^{-2}) and NEE (g C m^{-2}) estimates with those measured by the two Eddy Covariance stations in Finland (Hyytiälä and Sodankylä) during 2004-2008.

The performance of the applied models was assessed using the root mean squared error (RMSE), the relative root mean squared error ($RMSE_{\%}$), the absolute model bias, the relative model bias ($BIAS_{\%}$), and the coefficient of determination (R^2) by comparing the estimated values with the observed ones (Table 2). Also the leave-one-out cross-validation of the k-NN imputations (Study IV) was assessed with the above mentioned measures. The calculations were conducted using R Statistics (http://www.r-project.org/).

4 RESULTS

In Study I, the goal was to examine differences in mean height, diameter, basal area, and volume estimations obtained by different empirical simulators. Growth rates of these variables were simulated over 10 years using three different simulation chains: tree-level models, stand-level models, and a combination of these two. In Study II, the process-based static model was tested against the empirical model and the results were compared with the field observed annual growth of stem biomass. In Study III, the process-based dynamic model was run with both LiDAR and field input. The results were compared with empirical tree level simulations and field observed values. The tested variable was basal area growth. Attention was also paid to examining the reliability of the LiDAR derived input data. In Study IV, only the process-based model was utilized, since the examined variables contained annual carbon production. The accuracy of imputations with different number of nearest neighbours was compared. GPP and NEE estimations were compared with measured fluxes from the Eddy covariance towers in Hyytiälä and Sodankylä.

Comparison of different type of simulators

There were not any large differences between the tree- and stand-level empirical simulators (Study I). The mean height and diameter were predicted with a $RMSE_{\%}$ of 11.7-12.4% and 5.3-8.1 % in all the simulators. The RMSE% values of the basal area and volume estimations were moderately higher (12.5-19.8% and 17.6-24.4 %, respectively), than those for mean height and diameter. The relative bias when predicting mean tree height and diameter was small and also at a similar level among all the empirical simulators (for height, 4.4-5.4%, and for diameter, 0.1-1.7 %.), indicating a slight underestimation. The basal area and volume were also slightly underestimated in all the empirical simulators (basal area bias 0.6% to 4.5%, volume bias 1.0% to 4.4%). When examining the increment in the basal area during the simulation period, the tree-level empirical model proved to be notably less biased (bias of 2.5%) than the other simulators (bias 12.9-18.1%) (Table 3). All the reliability results (with n=597) for Study I can be found in Appendix 2.

Comparison of volume growth predictions obtained by the empirical and process-based simulators showed (Study II) that the precision of both approaches is at a similar level (RMSE of 33.4%-39.6% and *s* of 33.2-34.9%). (Table 3). The empirical model underestimated the growth with 18.8%, and the process-based model with 3.2%. In Study III, the basal area growth was overestimated in both the process-based simulators (bias% -1.5 to -11.4%); the least biased results were yielded by the empirical model (bias 0.4%).

Effect of different stand characteristics on growth estimations

When examining the annual stem biomass growth (kg DW ha^{-1} yr^{-1}) in Study II, the process-based model seemed to work best with Scots pine (bias 0.1%, RMSE% 32.1%) and Norway spruce (bias 1.9%, RMSE% 39.1%), respectively, indicating a slight underestimation, whereas for deciduous trees the results were worse ($RMSE_{\%}$ 62.7 %, bias 13.7%). Species specific examination of the results (Study I) shows that also the empirical tree-level models produce more accurate results for Scots pine and Norway spruce strata than for deciduous strata (Table 4).

Table 3. RMSE% and BIAS% of stand volume, stem growth, and stand basal area obtained with different simulators.

Variable	Model	RMSE%	BIAS%	s%	Unit	Data	N. of plots	Study
Basal area growth	Empirical, tree-level	59.5	2.5	59.4	$m^2ha^{-1}10\text{-}yrs^{-1}$	NFI	597	I
	Empirical, stand-level	50.0	12.9	48.3	$m^2ha^{-1}10\text{-}yrs^{-1}$	NFI	597	I
	Empirical, combined	79.2	18.1	77.1	$m^2ha^{-1}10\text{-}yrs^{-1}$	NFI	597	I
Stem volume growth	Empirical, tree-level	39.6[1)]	18.8[1)]	34.9[1)]	$m^3ha^{-1}1\text{-}yr^{-1}$	NFI	126[1)]	II
	Process, stand-level	33.4[2)]	3.2[2)]	33.2[2)]	$m^3ha^{-1}yr^{-1}$	NFI	138[2)]	II
Basal area growth	Empirical, tree-level	28.6	0.4	28.6	$m^2ha^{-1}5\text{-}yrs^{-1}$	Matalan-salo	52	III
	Process, field input, stand-level	38.1	-11.4	36.4	$m^2ha^{-1}5\text{-}yrs^{-1}$	Matalan-salo	52	III
	Process, LiDAR input, stand-level	39.3	-1.5	39.3	$m^2ha^{-1}5\text{-}yrs^{-1}$	Matalan-salo	52	III

[1)] n=126, which includes the plots used both in Study I (empirical simulations available) and Study II. Empirical volume growth estimate is annual average of the first 5-year growing period. In Study II the empirical volume growth estimate used in the comparison was the annual average of the whole simulation period . [2)] n=138, which includes all the plots used in Study II. Volume growth refers to the first year's growth estimate.

Table 4. The accuracy of estimated species specific basal area growth (m^3 ha^{-1} 10-years^{-1}) estimations obtained by the empirical tree-level model (Study I) and species specific stem growth (kg DW ha-1 yr-1) estimations obtained by the process-based static model (Study II).

	Empirical model (Study I) (n=597)				**Process-based model (Study II) (n=138)**			
Stratum	n	$RMSE_{\%}$	$BIAS_{\%}$	s%	n	$RMSE_{\%}$	$BIAS_{\%}$	s%
Scots pine	477	72.1	5.7	71.9	99	32.1	0.1	32.1
Norway spruce	389	77.7	-21.6	74.6	76	39.1	1.9	39.1
Deciduous	322[1)]	131.7	43.0	124.5	48	62.7	13.7	61.2

[1)] Only White birch strata included

When examining the results in terms of soil types, one can see that the tree-level empirical model was the most stabile one in different soil types, while in the stand-level empirical models the variables were underestimated to a greater extent on fertile sites than on dryer sites (Study I) (Fig. 4). In Study II the tree-level empirical model produced underestimates of volume growth for all the site types, while in the process-based simulations the bias indicated underestimation for the most fertile site, OMT, and overestimation for the other site types (Fig. 5).

With all the empirical simulators, the height estimates seemed to be least biased in the stands with small trees, the underestimation apparently increasing with tree height (Study I). The diameters and basal areas were overestimated with the smallest diameter classes and slightly underestimated in the larger trees. A similar trend was found in Study III using the process-based model, where a tendency to overestimate the growth of small trees and to underestimate the growth of bigger trees was detected with both field and LiDAR data. Using the process-based static approach (Study II), no strong age related trends were detected, but a slight tendency to underestimate growth most in the young stands was detected, especially at the stratum level.

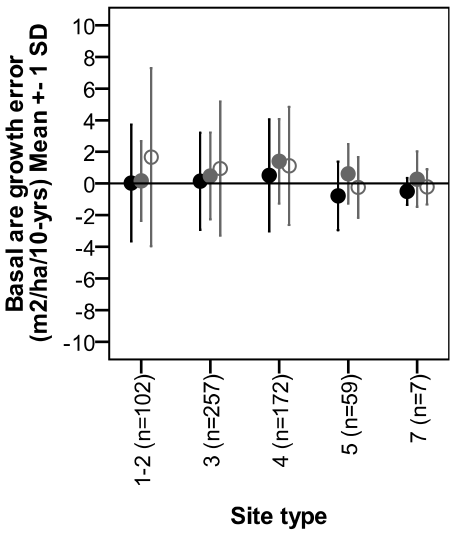

Figure 4. The soil type specific* mean and standard deviation of stand basal area growth estimation error (measured-modelled stand basal area growth, m^2 ha^{-1} 10-years^{-1}) in Study I as obtained using the tree-level simulator (black), stand-level simulator (grey), and combined simulator (white). *1 = herb-rich forest, 2 = herb-rich heath forest, 3 = fresh heath forest, 4 = dryish heath forest, 5 = dry heath forest, 6 = barren heath forest, 7 = rocks and sands.

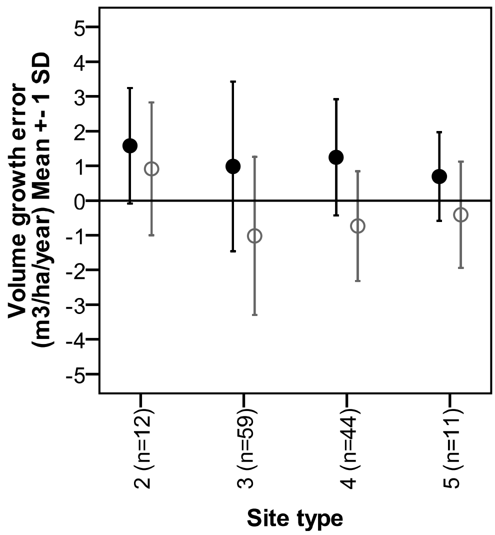

Figure 5. The soil type specific* mean and standard deviation of stand volume growth estimation error (measured-modelled stand volume growth, m^3 ha^{-1} year^{-1}) as obtained using the process-based model (grey) and empirical tree-level simulator (black), including the plots that were present in both studies I and II (n=126). *1 = herb-rich forest, 2 = herb-rich heath forest, 3 = fresh heath forest, 4 = dryish heath forest, 5 = dry heath forest, 6 = barren heath forest, 7 = rocks and sands.

Accuracy of LiDAR-derived input data

In Study III, the process-based model was tested both with field and LiDAR input data. The LiDAR derived input data seemed to be well in line with the field input data for mean tree height. Instead, the crown base height estimations in the LiDAR data differed considerably from the corresponding field measurements. In general, the crown volume and leaf biomass estimates based on the LiDAR data were higher than those derived from the basic field measurements (Figure 6).

Reliability of the k-NN Imputation

In Study IV, the stand level annual growth was simulated in the static process-based model complemented with the soil carbon estimation model Yasso07 using the NFI data from 2004-2008. Weather data was available from the corresponding years. The estimations were imputed for two large areas in Finland based on Landsat 5 TM images. Accuracy of the k-NN imputations was slightly better in the Central Finland than in the Lapland data set (Table 5). There were no remarkable differences between the imputations with different band sets. The bias of GPP and NPP was lowest with imputations using all of the bands. In contrast, RMSE was at its lowest in the imputations based on 2 different images and DEM. When examining the distribution of imputed values, one can see that the imputations tend to average the results compared to the original reference distribution (Fig. 7) and that the results taper with an increasing *k* (Fig. 8). The overall bias decreased with an increasing *k*, though in Lapland the GPP bias started to increase for MT and CT site types when *k*>9. The relative bias and RMSE of GPP imputations were notably higher ($bias_{\%}$ -30.5%, $RMSE_{\%}$ 49.3%) for CT site types than for the other site types in Central Finland. In Lapland, the site fertility did not affect accuracy. In Central Finland, GPP was notably underestimated ($bias_{\%}$ 8.2%) in deciduous dominated stands, while in the Scots pine and Norway spruce stands it was slightly overestimated ($bias_{\%}$ from -0.5 to -2.0%).

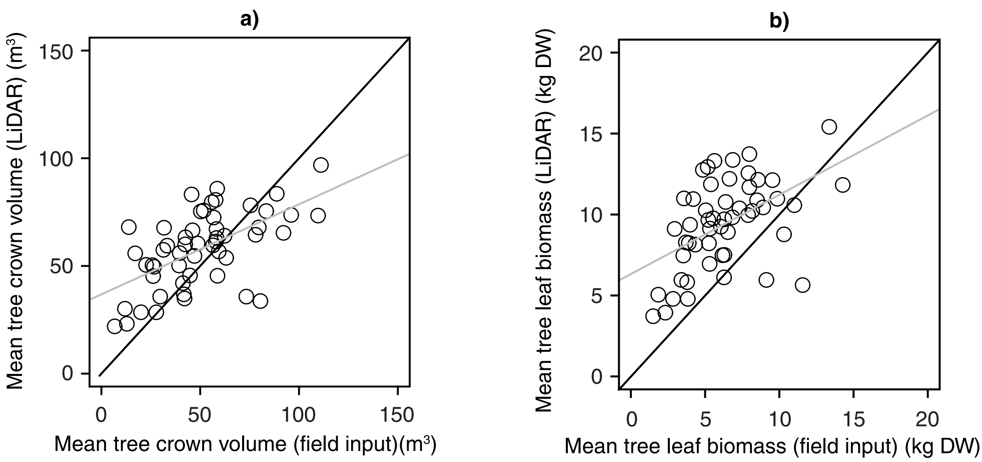

Figure 6. Stand crown volume (m^3 ha^{-1}) (R^2=0.35) (on the left) and mean leaf biomass (kg DW) (R^2=0.25) (on the right) as estimated from the LiDAR data and plotted against the field estimates. All the values are from 2004.

In Lapland, the Scots pine dominated stands were the least biased ones ($bias_{\%}$ of 1.4%), GPP being overestimated with Norway spruce (bias% -16.5%) and underestimated with deciduous trees ($bias_{\%}$ of 14.9%). According to simulations, the stands with a low basal area were more often carbon sources than those with a high basal area. The simulated GPP estimates increased more with increasing basal area than those obtained with imputations. The imputations seemed to more likely produce overestimations for stands with a low basal area and underestimations on the stands with a higher basal area.

Table 5. Cross-validation of carbon flux imputations (g C $m^{-2\ -yr}$) in Lapland and Central Finland in 2007 based on different independent variables.

	Central Finland (n=1072)	**Lapland (n=365)**			
	Bands 1-5 & 7, 1 image	Bands 1-5 & 7, 1 image	Bands 2-4, 1 image	Bands 2-4, 2 images	Bands 2-4, 2 images, DEM
GPP (g C $m^{-2\ -yr}$)					
Bias	5.6	0.8	3.9	1.7	-1.3
Bias%	0.6	0.2	1.0	0.4	-0.3
Rmse	240.1	136.8	144.2	146.4	135.7
Rmse%	27.0	35.6	37.5	38.0	35.3
Average k-NN	883.3	384.0	380.9	386.1	383.2
Average reference	888.9	384.8	384.8	384.8	384.8
NPP (g C $m^{-2\ -yr}$)					
Bias	0.2	0.2	1.6	0.7	-0.8
Bias%	0.1	0.1	0.9	0.4	-0.4
Rmse	111.1	64.5	67.2	68.3	63.7
Rmse%	29.7	35.9	37.4	38.0	35.5
Average k-NN	374.4	179.4	178.0	180.4	178.9
Average reference	374.6	179.6	179.6	179.6	179.6
NEE (g C $m^{-2\ -yr}$)					
Bias	1.3	0.6	-1.0	0.7	3.0
Rmse	94.1	52.0	53.3	53.8	49.2
Average k-NN	-156.0	4.9	6.5	2.5	4.8
Average reference	-154.8	5.5	5.5	5.5	5.5

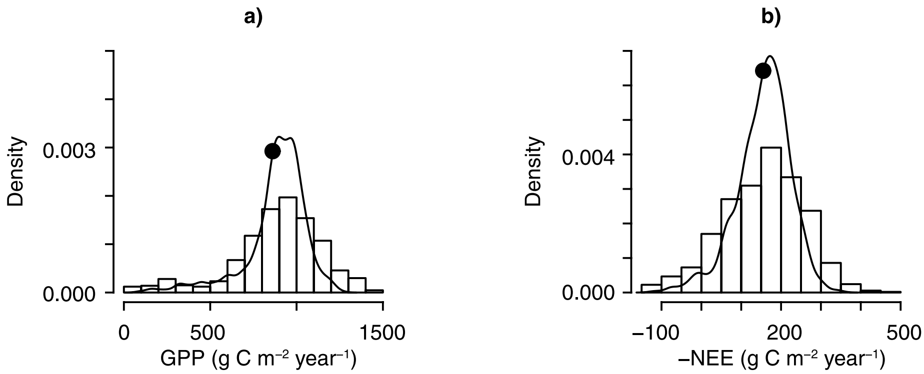

Figure 7. Distribution of GPP (left) and -NEE (right) in Central Finland. The black bars denote the reference values and the black line the imputation with k=5, bands 1-5 & 7 were used as independent variables. The black dots denote the k-NN imputations (with k=5) on the Hyytiälä site for 2007.

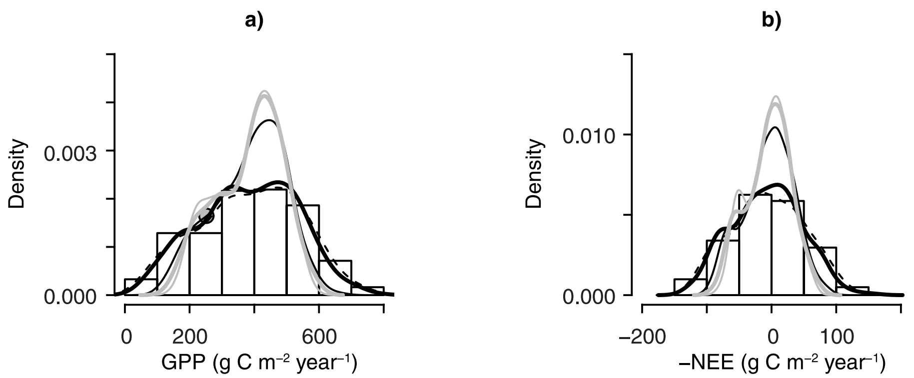

Figure 8. Distribution of reference and imputed values of GPP (left) and -NEE (right) in Lapland for 2007. The black bars denote observed values, the thick black line denotes imputations with k=3, the thin black line denotes imputation with k=5, the thick grey line denotes imputation with k=7 and the thin grey line imputation with k=11. Bands 1-5 & 7 were used as independent variables. The dots denote the k-NN estimates (k=5) on the Sodankylä site for 2007.

The imputed GPP values around the Sodankylä and Hyytiälä eddy flux towers were remarkably lower than the GPPs from the eddy measurements (Figure 9). The simulated GPP estimations followed a similar annual trend as the GPPs from the eddy covariance measurements, but in Sodankylä there was a remarkable decrease in the measured GPP in 2007, which was not found in the simulations. Also, the simulated NEE values were in line with the corresponding Eddy flux values in Hyytiälä, except for 2008, where in contrast to simulations, the observed NEE remained at the same level as during the previous year (Figure 10). The imputed NEE values, instead, were significantly smaller than the measured ones. In Sodankylä, the imputations were well in line with the EC measurements (Figure 10), while the simulations were biased but followed a similar trend as the measured NEE. According to both the simulations and imputation, the Hyytiälä plot was a carbon sink during 2004-2008. In Sodankylä, the plot is a carbon source according to the eddy flux measurements and imputations, but a sink according to the simulations.

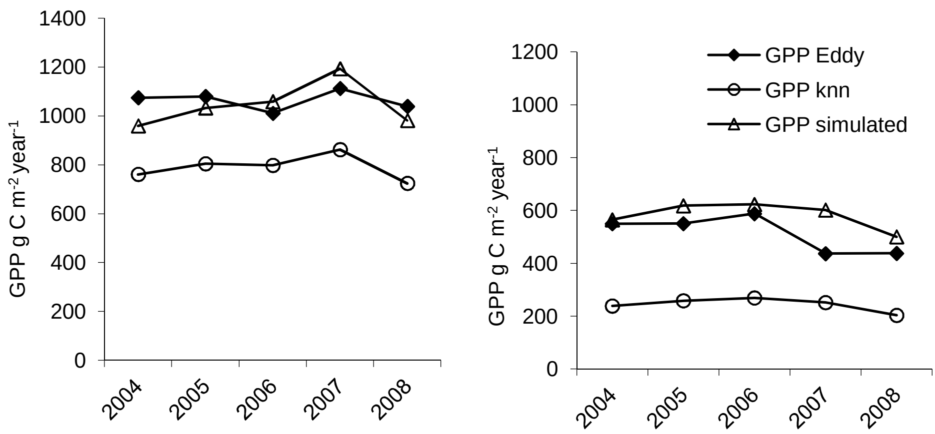

Fig. 9. Imputations and eddy flux measurements of annual GPP (g C m^{-2} year^{-1}) in Hyytiälä (left) and Sodankylä (right) during 2004-2008.

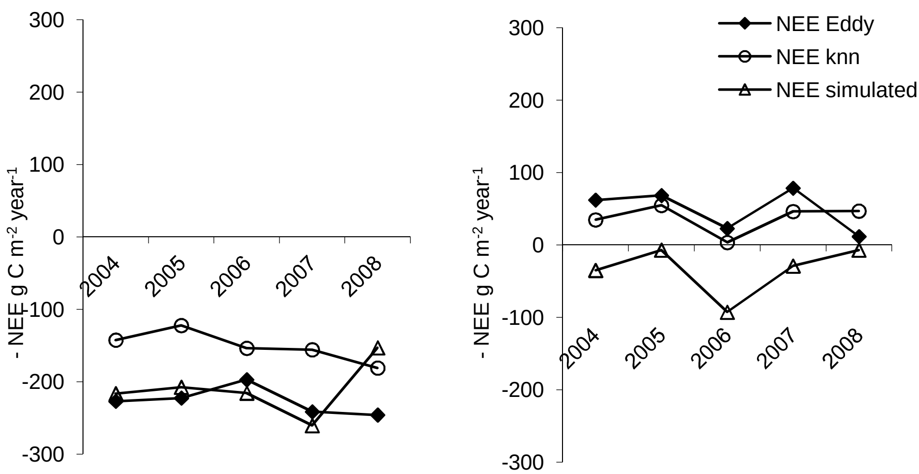

Fig. 10. Imputations and EC measurements of annual NEE (g C m^{-2} year^{-1}) in Hyytiälä (left) and Sodankylä (right) during 2004-2008.

5 DISCUSSION

This study demonstrates a new approach to growth estimation, where climate-sensitive process-based models are applied with easily available input data from field or LiDAR sources. The approach was connected with Landsat TM 5 satellite images, which allow producing of maps e.g. of forest carbon balance estimations for large areas in Northern Europe. Several data sets, mainly from the National Forest Inventory in Finland, were used to evaluate different forest growth simulators, both empirical and process-based, each containing a full set of models for estimating the entire growth process.

Study I evaluates the most commonly used Finnish empirical growth models at tree and stand level. In the other studies (II-IV), the process-based approach is applied in order to obtain growth predictions. In the most important role is a new process-based approach, which was developed for estimating forest growth by means of summary models. The method accounts for the site specific climate and its effect on tree growth at stand level through photosynthesis, respiration, and carbon allocation. Three versions of the summarized process-based approach were tested in this thesis: 1) a simple static approach (Study II) suitable for one-year carbon production estimation, and 2) a dynamic version complemented with a bridging model by Valentine and Mäkelä (2005) (Study III), which enables growth estimations of tree dimensions over longer periods of time, and 3) a static version complemented with the Yasso07 soil carbon dynamics model (Tuomi et al. 2008, Tuomi et al. 2009) (Study IV). In studies I and II, the input data was from the field (NFI), whereas, in the other studies, remote sensing data was also used. In Study III, the process-based simulator was tested with LiDAR data as input, and in Study IV the process-based estimations were extended to regional level by using the k-NN imputation with Landsat TM 5 satellite images.

Previously, the empirical simulators have had advantage over process-based models, because they are more accurate, if the climatic conditions and management schedules stay similar as those, which prevailed in the past. Further, the process-based models have been found to be impractical due to their complex structure and due to their need for difficult parameterisation. The advantage of the summarised forest growth estimation approach over the more complex process-based approaches is that its parameters and inputs are readily available for forest stands across the country. Therefore, they can be applied as easily as the empirical models, if climate data or corresponding estimates are available. In Finland, such data is available for the whole country since the 1960's from the Finnish Meteorological Institute in form of a 10 x 10 km grid. In the current approach, almost all of the parameter values of the models were available from previous studies on the individual summary models (for example, Mäkelä et al. 2008b, Duursma and Mäkelä 2007). Some of the parameters were readily available through model simulations. Based on the findings in studies II-IV, the summary model approach seems to be a potential tool at least for short-term forest growth predictions in Finland and nearby areas. However, there are several drawbacks and development needs in the current process-based approach, which are discussed in the following sections.

Comparing the accuracy of the simulators

Estimations by the empirical simulators were compared with the field data from NFI permanent sample plots (Study I), the focus being on the forest attributes at the end of the 10-year simulation period. The final state was selected as a baseline for the comparisons, as updating of the forest resource data is in important role in forest management planning. For comparison, the increment in the stand basal area during the simulation period (calculated using the data from the Study I) was included in the summary of this thesis.

All the empirical simulators provided fairly good estimates for tree diameter and height, while the estimates for basal area and volume were on average slightly poorer. Overall, the differences between the simulators were small. The combined simulator was the least biased of the tested simulators in the diameter estimations and the volume was estimated least biased with the stand simulator, while the basal area and height were estimated least biased with the tree simulator. When examining estimates of the basal area growth the least biased was clearly the tree simulator. The biases of mean height, diameter and stand basal area were similar to those obtained by Mäkinen et al. (2008). The empirical model predictions for the birches were notably less reliable than those for Scots pine or Norway spruce. It should be noted, that the regeneration of the new trees was not included either in the simulations or when calculating the field reference data, as the data for the smallest trees ($D_{1.3}$<4.5cm) was available only for the trees, which were considered as qualified by the measuring person. This means, that some of the smallest trees have falsely excluded from the data, which can have increased uncertainty in the results of the young stands with lot of trees around that size (Studies I and II).

Geographically, the tree and stand level empirical simulators behaved similarly, the volume error varying between different parts of Finland. The highest overestimations in the stand volume were found in certain areas in Southern and North-Eastern Finland. In the northern part, the forests were exceptionally old (>150 years) in the areas where the overestimations were the highest. This can be linked to problems in predicting stand-level mortality reliably. The findings were in line with a study by Sironen et al. (2008) in Southern Finland, where a non-parametric estimation method was compared with the tree-level models of Hynynen et al. (2002). In their study, the tree-level models overestimated the basal area growth in Southern Finland, while in the north the basal area growth was mainly underestimated. When examining the results of Study IV, one can see that the process-based GPP estimations are mainly in line with the EC measurements both in Hyytiälä and Sodankylä, but the NEE estimations for the Hyytiälä (Southern Finland) site are much closer to those measured by EC than in the Sodankylä site (Lapland). Even though there were only two EC sites from Finland available, the results indicate that applying the approach to Northern Finland requires further model development and parameterisation.

The growth estimates produced by the different process-based versions, including the static and dynamic versions (Study II and III), were generally in line with the field observations. When comparing the process-based volume growth (Study II) and basal area growth (Study III) estimations to those of the empirical growth models commonly used in forest planning in Finland, one may conclude that the reliability of the volume estimations of the static process-based approach is at the same level in the given data set. In Study II, the growth estimates were generally in line with the stem biomass growth derived from the NFI volume development, but the precision of the predictions was not very high (RMSE 34.3 %). The bias of the process-based estimates varied with tree species, stand age, and site fertility. The stem biomass growth was underestimated for the young stands; a potential explanation for this is the fact that mean annual growth was determined using the stand characteristics in the first measuring year (1985) but compared against field observed mean annual growth during a 10-year period. In the young stands, the leaf biomass is increasing rapidly, while in the older stands leaf mass is more stable (Sprugel 1984). There were also differences in the reliability of the model for different site types. The model highly underestimated growth in the most fertile sites (OMT), but for the other site types the biases were much lower. One reason could be that the scaling parameters estimated using the PipeQual model may not be sufficiently accurate for the OMT sites. Also, the study material contained only a few OMT sample plots.

In Study II the accuracy of the process-based model predictions was even slightly better than that provided by the empirical tree-level models (Hynynen et al. 2002). Instead, in Study III the empirical model was the more accurate one. In both cases the process-based model produced higher growth estimates than the empirical model. In Study II the selected sample plot set remained rather small due to high requirements for the stand characteristics and data availability. Only the mineral soil plots, which contained all the required sample tree measurements for all the existing strata, and which were free of mortality and thinnings, were selected to the study. Therefore, the sample plot set might not represent Finnish forests very comprehensively, which might be the reason for the biased empirical model estimates. It should also be noted, that there were differences between the initialisation procedures of the different model types, which caused variation in the initial status of the stands. The process-based model utilised the measured crown base height data, whereas in the empirical SIMO simulator the crown base heights were estimated using a crown ratio model (Hynynen et al. 2002). Further, different tree height calibration routines were used in the SIMO (stratum-wise calibration) and in processing of the NFI reference data (stand-wise calibration), which caused slight differences in the estimated initial stand volumes. This might have added some uncertainty to the empirical volume growth comparison presented in Study II, because the empirical mean annual growth was calculated based on the final volume simulated by the SIMO and the initial volume estimated based on the NFI data. It would be more appropriate to compare them with the empirical model's mean annual volume growth estimated directly by the SIMO simulator for the first 5-year period (see Fig. 11). In that case the empirical volume growth estimate decreased 0.2% on average from the mean annual 10-year growth estimate used in the Study II, the RMSE and bias staying around the similar level ($bias_{\%}$ of 18.8%, $RMSE_{\%}$ of 39.6%, $s_{\%}$ of 34.9%).

In Study III, the $RMSE_{\%}$ and $s_{\%}$ of basal area growth estimates remained rather high in all the tested approaches (28.6-39.3%). The bias was low in the empirical model (0.4%) and the process-based approach with the LiDAR data (-1.5%), while the results of process-based model with field input were overestimated by 11.4%. Overall, the accuracy of the growth estimates was similar to those from previous studies conducted in Finland. In Study I the reliability of empirical model (Hynynen et al. 2002) estimations was examined using a large data set from the national forest inventory plots in Finland. The basal area growth estimates calculated using the data set of Study I (Table 4) show, that the estimations were the least biased with the tree level model (2.5% overestimation), while the combined model estimates were the most biased (18.1% underestimation). The RMSE% of the basal area growth (50.0-79.2%) estimates was remarkably higher, than that obtained in the study III (28.6-39.3%). However, one should keep in mind that the growth results of study I contain extra estimation error caused by natural mortality, while in the studies II and III tree mortality did not occur in the sample plots. This explains the higher RMSE% of the basal area growth estimates in the study I. In Study II, the process-based model estimates were compared with NFI data, resulting in a $RMSE_{\%}$ of 34.3% and a $bias_{\%}$ of 2.1% for stem volume growth. The growth estimates obtained using the most similar neighbour method with the Finnish data have been at a similar level (Sironen et al. 2008).

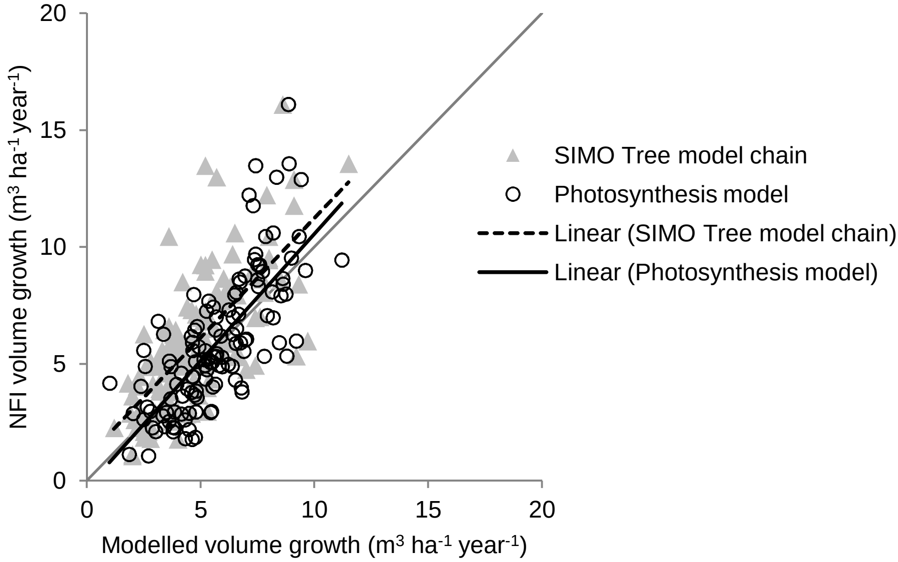

Fig. 11. Comparison of the stem volume growth estimations of the process-based model (black line, y = 1.0865x – 0.3066, R2=0.55) and the tree-level growth model included in the SIMO simulator (dotted line, y=1.0239 x + 0.992, R^2=0.51). The SIMO growth estimate is here the mean annual volume growth during the first 5-year simulation period (based on the initial stand status determined by the SIMO simulator).

In earlier studies, the pipe model based foliage biomass estimations have been tested, for example, by Berninger et al. (2005), who did not find any clear trends with respect to stand age, density, or site type with Scots pine, and by Lehtonen (2005), who reports the pipe model being the least biased for spruce stands in Finland, when tested with several empirical models. However, it would be worthwhile to test the pipe theory derived biomass predictions against more recent empirical biomass models for individual trees that are now available for Finland (Repola et al. 2007). Comparison of the reliability of the process-based approach with other related studies in Finland, for example, the hybrid model by Nuutinen et al. (2006) and Matala et al. (2006), is rather difficult, because those studies focus on the long-term simulation results in elevated temperatures and CO_2 concentrations, rather than on evaluation of the model results with measured data.

Overall improvement needs of current growth simulators

Forest growth simulators typically consist of applying several models starting from input data processing and ending up to a collection of sub-models used in the growth prediction. Therefore, problems in some part of the data processing and simulation chain can have a strong impact on the results. For the current empirical models, the changing climate and different management regimes can raise problems in the future. It is evident that purely empirical-based models need to be combined with hybrid solutions containing mechanistic processes in order to produce reliable estimations with varying climate scenarios. Empirical and process-based approaches have common problems especially when simulating far to the future. The longer the simulating periods are, the more important role the used mortality and regeneration models will get. These components exist in the tested tree-level empirical models, but they require still further development. The tree-level models (Hynynen et al. 2002) consider natural mortality caused by competition or age. Even though these models implicitly include average mortality caused by diseases, insects, snow damage, or storms, they were build based on data only from even-aged and single-species stands from mineral soils. Therefore, these mortality and self-thinning models can be assumed to function rather unreliably in the case of stands of irregular structure (numerous tree species, uneven spatial structure, and/or uneven size distribution) (Hynynen et al. 2002). In addition, while these above-mentioned phenomena occur, the consequences for the individual plot or stand can be destructive, which causes also high prediction errors in growth estimations in such plots. Instead, the stand-level models in their original form assume that natural mortality does not occur at all. Removal of trees by cutting is assumed to take place, however, and thus the basal area and volume estimates can be considered reliable only in the case of "normally" thinned forests.

There are also several development needs in the used process-based approach. The current approach did not include any mortality or regeneration models, due to the short simulation period. One of the aims for future research is to link the summary approach with mortality and regeneration models, which would allow simulating the stand growth over longer time periods. Additionally, special attention should be paid to modelling development of young trees, as well as deciduous trees (Study II). Another goal is to include nitrogen and water uptake processes in the simulator (Mäkelä et al. 2008a, Duursma et al. 2008), which would improve reliability of the allocation procedure and, obviously, reduce differences in model errors between site types, as stated in Study II. In the current version, nutrient availability was present only through site fertility parameters, which affected carbon allocation to fine roots, and implicitly through the leaf area, which was derived from the NFI data. As photosynthetic production rate has been reported to increase with N content of leaves (Ågren 1996, Smith et al. 2002), this response should be improved in the model. As the soil properties and topography especially affect the water and nutrient balance of the forests, it would be worthwhile to test soil maps and a digital elevation model as model inputs, since these are available for the whole of Finland (http://www.geo.fi/).

The current version has been parameterised only for mineral soils, and its parameterisation for peat lands would be required in order to expand its usage to all boreal forests. Further, as stated previously, the model performance especially in relation to soil processes was not very good in the Sodankylä sample plots, which suggests that the model parameters should be adjusted for northern areas. The current version of the model was only tested under prevailing climatic conditions, and in the case of applying it with raised temperatures, the model response to elevated CO_2 concentration in the air should be further adjusted. Also, generalisations of the relationship of, for example, temperature sum and P_0 are only valid in climates similar to Finland. It should be noted, that the P_0 estimation based on temperature sum (Study II) gives only rough estimates based on average weather conditions. Further, as the hierarchical structure of the modelling data (different sites containing data from different years) was not taken into account when building the temperature-sum-based P_0 model, it can not properly differentiate the variation between the different years. Therefore, if local annual weather data is available, P_0 should be calculated based on that.

Needs to improve the LiDAR based version

Based on the findings of Study III, the LiDAR based approach produced reasonable results despite of a tendency to overestimate crown volumes. However, there were several drawbacks and inaccuracies in the current approach, which should be addressed in future development. The most crucial need is improvement in the crown volume estimation and its conversion to leaf biomass. In Study III, the crown volume estimation employed a triangulation and alpha-shape based approach that has earlier been successfully applied to species recognition (Vauhkonen et al. 2009), predictions of stem attributes (Vauhkonen et al. 2008), and crown base height estimation (Vauhkonen 2010). Here, this methodology led to overestimated crown volumes, and thus to overestimated leaf biomasses. Estimating the number of trees per plot could actually be ignored by estimating the tree level crown volumes directly for all the trees in the plot either by using single tree detection methods or by the k nearest neighbour imputation (for example, Packalén and Maltamo 2008) and applying them with the tree level leaf biomass equations.

One obvious reason for the inaccuracy in the crown volume estimation was the low pulse density (0.7 m^{-2}) of the LiDAR data used. Even though findings in several studies show that the accuracy of stand-level estimations of, for example, stem volume based on distribution of the ALS based height values does not remarkably decrease with a decreasing pulse density (for example, Maltamo et al. 2006, Gobakken and Næsset 2007), according to Vauhkonen et al. (2008), a density of at least 3 pulses m^{-2} would be required when attempting to predict the species and stem diameter of individual trees using crown structural attributes. Despite of a low pulse density, the estimated mean crown volumes were fairly well in relation with the reference values, at least when compared with the crown base height estimation. It should be noted that the estimations obtained by the LiDAR based version contain both under and overestimations in the sub-models, which has to be considered when examining the accuracy of the final results. Because the stand total crown volume and number of trees per hectare were overestimated in the LiDAR version, the reliability of the mean tree crown volume estimates also is exaggerated.

As the estimates based on the field data also contained some uncertainty, it is rather difficult to verify the real origin of the estimation error. Some inaccuracy is related to the field measured growth, which was based on drilled samples, which were only from the dominant tree class. Therefore, the generalised plot-level field growth might have been overestimated. Because the field reference of the tree growth was determined based on the generalisation model using only one calibration tree per stratum, the plot-level field growth values contain also remarkable random variation. It should be noted, that the model for generalising the field growth ignored the bark growth, but this effect was assumed to be very small during such a short growth period. However, according to Ilvessalo (1965) the bark growth of Scots pine can be 5-20% of the diameter growth, depending on the tree shape and diameter, the share being highest with the smallest trees.

Only a few of the countless possibilities that LiDAR data would offer for determining the canopy conditions were utilised in this study. For example, as the 3D LiDAR point cloud is available, shading properties in the canopy could be derived directly from it. This could be applied, for example, to the effective extinction coefficient used in the process-based approach (Duursma and Mäkelä, 2007), which was derived here from the estimated mean tree crown dimensions. When applying the approach to mixed forests, species specific input data should be derived from the LiDAR data. This could be done by applying the area based approach with the nearest neighbour procedure as introduced by Packalén and Maltamo (2007). Alternatively, one could incorporate tree species recognition into the procedure either by combining the LiDAR data with multispectral aerial images as suggested by Holmgren et al. (2008), or in case the LiDAR data is dense enough, using only the LiDAR data (Vauhkonen et al. 2008). The alpha shapes should also be compared with alternative methods of estimating the crown structure, such as the voxel based approach as introduced by Popescu and Zhao (2008). Further, the process of deriving the required input data should be tested with more versatile forest stands in the future. Now, the sample plots were only from Scots pine dominated forests. Problems may arise when applying the approach to young stands, where LiDAR based detection of crown dimensions may face challenges (Naesset and Bjerknes 2001). Conducting field based and LiDAR based forest inventory with leaf biomass and crown dimension measurements based on versatile sample plot data would be useful for future development purposes. In addition to improving the crown volume estimation method, further studies with more accurate LiDAR data and more versatile forest area would be required in order to make reliable conclusions on its applicability with the process-based model.

Generalisation with k-NN method

The nearest neighbour method (k-NN) can be used with satellite images either for producing missing input data for the areas to be simulated or for generalizing the already simulated results to the surrounding pixels. In this thesis, k-NN was used for generalizing the plot wise simulated results of annual carbon balance to the larger areas based on Landsat 5 TM satellite images. When examining reliability of the k-NN itself, the method seems to work well (Study IV). However, the tendency of the k-NN method to average the results is apparent in the results of Study IV, where the highest carbon sinks and sources were lacking among the imputed values. Further, the GPP imputations for the stands with a low basal area were remarkably unreliable, and with high basal areas, the imputed GPP started to saturate. Study IV showed also that the reliability of the imputations varied according to the site fertility and the main tree species in the stand, which indicates that the spatial variation in carbon production caused by these factors was not sufficiently detected based on Landsat images only. Employing other data sources in addition to Landsat bands, for example, soil maps or DEM-derived products, should be considered in order to improve the reliability of the imputations. Furthermore, aggregating the data from different years was found problematic. It is likely that the land use map from 2007 and the Landsat image from 2007 do not match with the NFI observations from 2004-2008 in all the areas due to thinnings, cuttings, or land use changes.

The timing of a satellite image is an important element which largely affects the reliability of the imputations. Several studies (for example, Rautiainen et al. 2009) have reported seasonal differences in reflectance of forests due to changes in biochemical properties, such as chlorophyll and water concentration in the vegetation. With satellite images, for example, MODIS (Moderate Resolution Imaging Spectroradiometer), earlier greening of the understory vegetation can be mixed with canopy greening (Wang et al. 2005, Rautiainen et al. 2009). Therefore, if the imputations are done with images taken at the very beginning or end of the summer in an area with long distances between the southern and northern borders, the reliability of imputations might differ remarkably between different parts of the area. In addition, the Landsat images represented the forests on only 1-2 days per year, while the simulated values of GPP, NPP, and NEE represented accumulations over the whole year, which is likely to cause uncertainty in the results. One solution to tackle the issue would be to base the imputation on longer time series of satellite images taken during the growing season. However, at least in Finland, it seems difficult to find such a good time series covering large areas with an acceptable level of cloud cover. The k-NN procedure used in Study IV could be improved in the future by adding weighting procedures (Tomppo and Halme, 2004) or by applying several images from the growing season. MODIS maps or EC measurements from the neighbouring countries could be utilized in the future to validate this approach.

The k-NN approach used in Study IV allows extending the estimations of, for example, carbon fluxes for all the boreal areas with similar climatic conditions as in Finland, for example, in Sweden, Norway, and northern parts of Russia, provided that the required weather data and NFI or equivalent data are available. As previously mentioned, the used process-based model has been parameterised only for mineral soils and for few tree species, and parameterisation for peat lands and additional tree species would be required to reliably extend estimations to all the boreal forests. As MODIS maps provide thematic maps on numerous different environmental variables, such as leaf area index, land cover, and land surface temperature, they could also be utilized with this approach, if such data is not otherwise available. MODIS maps have been utilized widely in recent studies both as input data for growth models or for evaluation purposes (Zhao et al. 2005, White et al. 2006, Coops et al. 2007). MODIS also offers NPP maps, which have been developed by utilizing an eddy covariance (EC) network and process-based models (Running et al. 2004). The disadvantage of the MODIS product, however, is its coarse resolution (1 km) and limited network of ground data, i.e. a sparse eddy flux network (Turner et al. 2006). Landsat 5 TM images (Study IV) enable a significant improvement of the output resolution. When using k-NN methods, the localization of the estimates has an important role (Sironen et al. 2008). Variation in vegetation and climate zones can vary within a satellite image (image size 170 x 185 km in Landsat 5 TM), and in order to reduce the effects of, for example, variation in rainfall to the carbon flux imputations, both the reference and target pixels should be from the same, relatively small area. Sub-areas included in the k-NN method could be defined based on the distance from the target pixel or by using segmentation methods, such as local indicators of spatial association (LISA), as introduced, for example, by Räty and Kangas (2010).

However, even though the reliability of the k-NN generalization seemed to be at an acceptable level, the reliability of the actual estimations for the sample plots still remains questionable. If the estimation method fails to predict the carbon balance of the sample population, the generalization will also fail. It is rather difficult to estimate the accuracy of the carbon balance estimations, as only two Eddy covariance measurement stations exist in the study area. Based on the comparisons of the simulated and observed carbon production in the Eddy sites, the Yasso07 soil carbon model seemed to work better in Southern Finland than in Northern Finland. The soil model simulations rely on several rough assumptions, which can have a considerable effect on the NEE estimates. The steady state simulation (for 10,000 years in this case) was conducted with assumed mean litter fall and weather conditions, which definitely can vary during such a long time span. The annual plot wise litter fall and weather conditions were assumed to remain similar during the whole simulation period, except for in the last few years, for which stand wise estimates based on NFI data were available. This simplification may have caused both under- and overestimation of annual litter fall, depending, for example, on stand age, site fertility and main tree species of the forest, as well as the prevailing weather conditions. Secondly, the possible cutting removals in the recent decades were ignored, as the data was not available. The mean steady state values obtained in Study IV (6.0 kg C m^{-2} for Central Finland) were in line with those reported by Liski and Westman (2005) and Peltoniemi et al. (2004), who observed average soil carbon pools of 5.8-9.6 kg C m^{-2} and 6.8 kg C m^{-2}, respectively, in Southern Finland. However, weather conditions and litter fall, especially during the latest simulation years, can cause large variations in the estimated carbon pool, and inaccuracies in these estimates are reflected in the NEE values. Therefore, estimating NEE with this approach is rather uncertain, especially if recent local weather data is not available. This is of particular concern when the uncertainty range lies at about zero, i.e., the stand may either be a sink or a source of carbon. Further investigation is required in order to assess the reliability of the method. Comparisons could be extended, for example, to Eddy covariance stations in Sweden. Additionally, other soil carbon models, such as ROMUL (Chertov et al. 2001), are available and could be applied instead of the Yasso07 model.

6 CONCLUSIONS

It is evident that there is a need for 1) developing forest growth estimation methods adaptable to both climatic and environmental changes, 2) developing methods capable of estimating the development of other than traditional stand characteristics, 3) improving the methods of utilizing remote sensing data with the new types of growth simulators, and 4) shifting towards open-source simulation frameworks that can be easily modified, updated with new models and linked with other systems in order to adapt them to the changing needs of the users. The climate-sensitive forest growth estimation approach introduced in this thesis (studies II-IV), as well as the open-source simulation frameworks, such as SIMO (Tokola et al. 2006) utilized in Study I, can be seen as promising efforts towards these goals.

The reliability of the empirical and process-based summary models tested in this thesis was at a similar level in the short run (Studies II and III). However, the process-based simulations were carried out using rather small data sets, which included mainly well-managed forests without natural mortality. Therefore, further testing of the process-based approach with a wider range of site types, tree species, mixed forests, as well as geographical areas is required in order to draw conclusions of their reliability in larger scale use. In longer simulations, the role of mortality and regeneration models becomes more important; this would require special attention and further developing efforts in both empirical and process-based approaches. As a conclusion, which model to use depends on the input data, simulation time, and the needs of the model user. As shown in Study I, there are not big differences between the empirical tree and stand-level models, and they remain the mostly used ones due to their long empirical background. However, in the case of warming climate or when testing new kind of management regimes, process-based approaches or hybrid models would obviously offer a more reasonable solution (see e.g. Miehle et al. 2009), given that they contain proper mechanisms to respond the changes in the environment and that they have been adequately tested. Based on the evaluations done in studies II-IV, the current summary approach seems to have potential for short-term predictions in even-aged mineral soil forests in the southern part of Finland. However, in order to apply the process-based approach to new kind of thinning schedules, for example, uneven-aged forest management, proper regeneration and mortality models should be applied and the estimation procedure should be conducted on tree level. Developing a mechanistic model system with a reliable regeneration and mortality system that responds to changing light, nutrient, and water conditions remains a future challenge.

In general, the approach seems to be a promising starting point and there is a wide range of possibilities to expand its usage. For example, estimating carbon fluxes for large areas based on LiDAR data would be a very interesting application and could be immediately tested, as the model contains components for estimating gross and net primary production as well as the soil respiration, which enables the estimation of the whole net ecosystem production. The approach presented in the thesis contains building blocks for developing an easily applicable visual tool in order to examine the effects forest management in changing environmental and climatic conditions for environmental and industry related decision making and policy making purposes. It could be easily integrated, for example, in the forest planning framework SIMO, which would allow accommodating for carbon balance issues in practical forest planning and optimisation tasks. It would also offer an interesting platform for future research purposes.

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Appendix 1.

Static process-based summary model

Tree growth is estimated at the stand level, based on carbon production and respiration in different components of the trees. Annual forest growth can be expressed as

$$P_N = r_{NPP}\ P, \tag{A.1}$$

where P_N is net primary production (NPP), P is gross primary production (GPP), and r_{NPP} is the ratio of the two, depending on the respective rates of maintenance and growth respiration of the stand. In studies II-IV, r_{NPP} was assumed to be proportional to mean stand height in accordance with the equation $r_{NPP} = 0.6 - 0.0113\ H_{mean}$, based on the findings by Mäkelä and Valentine (2001) (see Study II). Annual biomass production, G_t (kg DW ha^{-1} yr^{-1}) (DW=dry weight), is proportional to P_N as follows:

$$G_t = c_C^{-1} P_N\ , \tag{A.2}$$

where c_C is the carbon content of biomass dry weight ($c_C \approx 0.5$). P depends on environmental driving variables and forest stand data as follows:

$$P = f_{APAR}\ P_{0,} \tag{A.3}$$

where f_{APAR} is the (effective annual) mean fraction of photosynthetically active radiation (PAR) absorbed by the canopy, and P_0 is annual canopy photosynthesis in a (hypothetical) canopy that absorbs all PAR radiation.

According to the LUE based model (Mäkelä et al. 2008b), annual canopy GPP (P) can be expressed as

$$P = f_{APAR} \sum_{k=1}^{365} \left(\beta\ \Phi_k\ f_{Lk}\ f_{Sk}\ f_{Dk} \right), \tag{A.4}$$

where f_{APAR} is as above, β is potential daily LUE (kg C / mol), Φ_k (mol m^{-2}) is PAR above the canopy during the day k, and f_L, f_S and f_D are modifying functions of daily PAR, daily average temperature, and daily average vapour pressure deficit (VPD), respectively, that take values between 0 and 1 (see Härkönen et al. 2010 for details). Further, P_0, the (hypothetical) maximum canopy GPP, can be obtained with the eqn. A.4 when f_{APAR} =1.

Table A.1. Model parameters and their values. Version "D" denotes the dynamic version parameters used in Study III and version "S" the static version used in studies II and IV.

	Explanation	Unit	Scots pine
γ_b	Coefficient of allometric eqn. for branch length		0.386
b	Allometric exp. for mean branch length		0.8268
φ_B	Form coefficient		1.3
φ_C	Form coefficient of stem inside the crown		0.55
φ_S	Form coefficient of stem below the crown		$0.5(r_C + 1)/r_C$, where $r_C = L_C/H$
η_B	Foliage mass:basal area of branches	kg DW m^{-2}	350
η_S	Foliage mass:cross-sectional area at crown base [1)]	kg DW m^{2}	T_{mean} x 16 +440
α_{R2}	Fine root biomass:needle biomass on OMT [2)]	kg DW (kg DW)$^{-1}$	0.2
α_{R3}	Fine root biomass:needle biomass on MT	kg DW (kg DW)$^{-1}$	0.36
α_{R4}	Fine root biomass:needle biomass on VT	kg DW (kg DW)$^{-1}$	0.51
α_{R5}	Fine root biomass:needle biomass on CT	kg DW (kg DW)$^{-1}$	0.7
ρ_S	Wood density of stem	kg DW m^{-3}	400
ρ_B	Wood density of branches	kg DW m^{-3}	400
φ	Empirical parameter		0.4
k_H	Extinction coefficient for homogeneous stands		0.3
SLA	Specific leaf area	m^2 (kg DW)$^{-1}$	11
$m_{F,0}$	Maintenance respiration rate of foliage	kg C (kg C)$^{-1}$ yr^{-1}	0.7
$m_{R,0}$	Maintenance respiration rate of fine roots	kg C (kg C)$^{-1}$ yr^{-1}	0.3
$m_{W,0}$	Maintenance respiration rate of sapwood	kg C (kg C)$^{-1}$ yr^{-1}	0.075
z	Sapwood area:crown length	m^2 m^{-1}	2
c	Carbon used for growth respiration:NPP	kg C (kg C)$^{-1}$	0.3
v_F	Leaf longevity	years	3.5
v_R	Feeder root longevity	years	1
α_T	Coarse root biomass:stem biomass	kg DW (kg DW)$^{-1}$	0.22
β_S	Mean pipe length in main stem of crown:crown length	m m^{-1}	0.5

[1)] η_S is a linear function of annual mean temperature fitted with the results for Scots pine by Palmroth et al. (1999). [2)] Site types classified according to the classification system of Cajander (1925). CT=Calluna type (dry heath forest), VT=Vaccinium type (dryish heath forest, MT=*Myrtillus* type (fresh heath forest), and OMT=*Oxalis-Myrtillus* type (herb-rich heath forest). α_R for Scots pine was adjusted using the pine fine root:needle ratios of MT and CT presented by Vanninen & Mäkelä (2005) and Helmisaari et al. (2007).

Norway spruce	Birch and other deciduous trees	Source	Version
0.4614	0.2689	Mäkelä (1986), Mäkelä & Vanninen (2001), Vanninen & Mäkelä (2005)	S,D
0.5198	1		S,D
0.63	0.5		S,D
0.5	0.5		S,D
$0.5(r_C + 1)/r_C$, where $r_C = L_C/H$	$7.5946\ L_C^{0.658}$		S,D
400	216		S,D
T_{mean} x 16 +540	T_{mean} x 16 +245	Palmroth et al. (1999)	S,D
0.18	1	Vanninen & Mäkelä (2005), Helmisaari et al. (2007) [2)]	S,D
0.3	1.5		S,D
0.42	2		S,D
0.54	2.5		S,D
376	480	Kärkkäinen (2003)	S,D
590	550		S,D
0.4	0.4	Duursma & Mäkelä (2007)	S,D
0.3	0.3		S,D
10	12	Luoma (1997), Stenberg et al. (1999), Parviainen (1999)	S,D
0.7	0.7	Valentine & Mäkelä (2005)	D
0.3	0.3		D
0.075	0.075		D
2	2		D
0.3	0.3		D
-	-		D
-	-		D
-	-		D
-	-		D

In Eqns (A.3) and (A.4), we assume that f_{APAR} incorporates the effects of canopy structure on GPP and P_0 describes the effects of driving variables. Here, canopy structure is defined as the combination of LAI, its spatial distribution, and its shading properties. f_{APAR} can be approximated using the Lambert-Beer law with an (effective annual mean) extinction coefficient, k_H (Table A.1). Duursma and Mäkelä (2007) showed that the same exponential equation can be applied more generally to non-homogeneous canopies, provided that k_H is replaced by an effective extinction coefficient, k_{eff} (i denotes tree species strata):

$$f_{APAR} = (1 - e^{-\sum_{i=1}^{n} (k_{eff,i} L_i)}), \tag{A.5}$$

where k_{eff} depends on leaf area per tree, L_A (m^2), mean crown surface area, S_{A} (m^2), a homogenous extinction coefficient, k_H, and an empirical parameter, φ (Table A.1). The (all sided) leaf area per tree can be calculated as $L_A=a_{LS}W_F/N$, where a_{LS} is specific leaf area (SLA) (m^2 (kg DW)$^{-1}$), and N is stocking density (ha^{-1}). The specific leaf areas for different tree species were assumed constant (Table A.1). Mean crown surface area was calculated based on the measured (basal area weighted) mean crown length, L_C (m), and width, C_W (m), assuming the pine and deciduous crowns as ellipsoids and the spruce crowns as cones. In the field input version (studies II-IV), the stand leaf biomass, W_F, was estimated based on the empirical ratio of foliage mass to the stem cross-sectional area at the crown base A_C (m^2), which can be expressed as A_C =B $(L_C / (H-1.3))$, where B is basal area (m^2). The biomasses of other tree components, W_i (kg DW ha^{-1}), were estimated using allometric equations (see Table A.2). Site fertility was included in the estimation through site type specific foliage:fine root ratios using the site type classification according to Cajander (1925).

As each stratum contributes to canopy GPP (P_i) in the proportion of its effective leaf area, $L_{eff,i}$, defined as $L_{eff,i} = k_{eff,i}\, L / k_H$, stratum's GPP can be expressed as

$$P_i = s_i \; f_{APAR\_M}\, P_0, \tag{A.6}$$

where s_i is the ratio of the stratum specific effective leaf area, $L_{eff,i}$, to the sum of the effective leaf areas of all strata.

Dynamic process-based summary model

Annual carbon production (GPP and NPP) was estimated similarly as in the static version explained in the previous section. The growth of stem and crown dimensions (Study III) was estimated utilising the "bridging model" introduced by Valentine and Mäkelä (2005), which is based on the pipe theory. The growth rate of tree height was estimated as

$$\frac{dH}{dt} = g_1(H - H_C)\left(\frac{g_2 - (g_4 - 1)H_C - H}{g_3 + (g_5 - 1)H_C + H}\right), \tag{A.7}$$

where H_C is crown base height (m), and g_i:s are empirical parameters defined in Table A.3.

The crown rise rate was assumed to be

$$\frac{dH_C}{dt} = S(C)\frac{dH}{dt}, \tag{A.8}$$

where $S(C) = 0$, if $L_C < 7$ meters and otherwise $S(C) = 0.7$.

Crown width was assumed to stay proportional to crown length. Basal area growth at breast height (1.3 m) was determined on the basis of basal area growth at crown base. First, the total cross-sectional area at the living crown base, A (m^2 ha^{-1}), after one year growth can be expressed as

$$A_{t2} = A_{t1} + A_{t1}\left(\left(\frac{L_{C,t2}}{L_{C},t1}\right)^z - \left(\frac{H_{t1} - H_{C,t2}}{L_{C,t1}}\right)^z\right). \tag{A.9}$$

Further, the new basal area at the height of 1.3 m, B_{t2}, can be estimated based on A_{t2}, new height, and crown base height using the relationship in eqn. 11. The values of the structural parameters used in the estimation chain were obtained from empirical studies testing the above relationships (Table A.1). The LiDAR input and the field input versions of the process-based dynamic approach were the same, excluding the estimation of the initial leaf biomass (W_F), which was derived directly from the crown volume estimations in the LiDAR method (see Study III).

Estimating soil respiration and NEE

In Study IV, the soil respiration was estimated based on the annual litter fall data using the Yasso07 soil model (Tuomi et al. 2008, Tuomi et al. 2009). In Yasso07, the total litter fall is divided into non-woody and woody litter, which are further divided into four compound groups: 1) compounds soluble in a non-polar solvent, ethanol, or dichloromethane (E), 2) compounds soluble in water (W), 3) compounds hydrolysable in acid (A), and 4) compounds neither soluble nor hydrolysable at all (N). Each group has different decomposition rates, which depend on temperature and precipitation. Decomposition results in mass loss from the system and inside the system, as well as formation of more recalcitrant humus (H). The parameters used in the model are described in Study IV. The annual carbon change of soil, ΔC_S (g C m^{-2} $year^{-1}$), can be expressed as

$$\Delta C_S = C_{S,1} - C_{S,0}, \tag{A.10}$$

where $C_{S,1}$ (g C m^{-2} $year^{-1}$) is soil carbon at the end of the simulation year, and $C_{S,0}$ (g C m^{-2} $year^{-1}$) is soil carbon at the beginning of the simulation year. Net ecosystem exchange (NEE), E_N (g C m^{-2} $year^{-1}$), can be expressed based on NPP (P_N), the annual soil carbon change, ΔC_S, and carbon in the annual litter fall, L_T (g C m^{-2} $year^{-1}$), as follows:

$$E_N = -(P_N - L_T + \Delta C_S), \tag{A.11}$$

a negative NEE denoting that the forest is a carbon sink and positive that it is a carbon source. The model was first driven to steady state by simulating soil processes for 10,000 years for each plot before starting the actual simulation. The simulation to steady state was done in two parts. First, the Yasso07 model was run for t=10 000-t_S (years), where t_S is the stand age in the NFI plot data. The total annual litter fall in this first simulation part consisted of 1) average litter fall, L_L (kg DW ha^{-1}), from all the living trees in the NFI plots in the study area (Lapland and Central Finland areas separately) from 2004-2008, and 2) the average litter fall from dead trees and ground vegetation, L_{NG} (kg DW ha^{-1}), estimated as a function of the effective temperature sum in the plot (mean ETS during 1961-1990). The linear functions describing the relationship between ETS and L_{NG} were constructed based on average litter fall data from Southern and Northern Finland (see Study IV). The second part included running the Yasso07 model for t_S years with annual litter fall, which was interpolated between the mean annual litter fall L_L at moment t and NFI-based plot wise litter fall, L_{LS}, at moment t_S, assuming a linear relationship. The plot wise weather conditions were assumed to be the same as the mean weather during 1961-1990 of the nearest point in the FMI 10 x 10 km data grid, except for the last 10 years of the steady state simulation, which were run with the annual weather data.

Annual litter fall, L_{LS}, was estimated on the basis of turnover rates defined in Study IV by Liski et al. (2006) using the biomass estimations of the NFI plots obtained with the process-based model. For Southern Finland, the annual foliage turnover rates for Scots pine, Norway spruce, and deciduous trees were 0.22 (0.1), 0.1 (0.05), and 0.78, respectively (values for Northern Finland in brackets). The annual branch turnover rates for Scots pine, Norway spruce, and deciduous trees were 0.02, 0.0125, and 0.0135, respectively. The corresponding turnover rates for coarse roots were 0.0184, 0.0125, and 0.0135. For fine roots, the turnover rates were 0.868, 0.811, and 1.0, respectively. The estimated average soil carbon in the steady state in 2007 in the Lapland plots was 6.6 kg C m $^{-2}$ and in Central Finland 6.0 kg C m^{-2}. The average of the total annual litter fall in Lapland was 159 g C m^{-2} and in Central Finland 203 g C m^{-2}.

Table A.2. Biomass equations based on the pipe theory (Mäkelä 1986, Kantola and Mäkelä 2006, Ilomäki et al. 2003).

Variable	Equation	Unit
Leaf biomass	$W_F = \eta_S A_C$	kg DW ha^{-1}
Branch biomass	$W_B = \varphi_B \rho_B (C_W / 2) \eta_S / \eta_B A_C$	kg DW ha^{-1}
Stem biomass	$W_S = \rho_S (\varphi_S H_C A_C + \varphi_C L_C A_C)$	kg DW ha^{-1}
Fine root biomass	$W_{FR} = \alpha_R W_F$	kg DW ha^{-1}
Coarse root biomass	$W_{CR} = \alpha_T W_S$	kg DW ha^{-1}

Table A.3. Equations used in height growth estimations in the dynamic version.

Equation	**Explanation**
$g_1 = 1/(1+z)/(g_0/(\beta_1 \rho_W (1+c))$	Parameter
$g_2 = \left(\frac{\rho_F(s_0 - m_F) - \rho_R m_R}{g_0}\right) - \left(\frac{1+c}{g_0}\right)\left(\frac{\rho_F}{v_F} + \frac{\rho_R}{v_R}\right)$	Parameter [1)]
$g_3 = \left(\frac{z}{1+z}\right)\left(\frac{\rho_F + \rho_R}{\rho_W \beta_1}\right)$	Parameter
$g_4 = 1 + \left(\frac{\rho_W m_W \beta_2}{g_0}\right)$	Parameter [1)]
$g_5 = \left(\frac{z}{1+z}\right)\left(\frac{\beta_1 + \beta_2}{\beta_1}\right)$	Parameter
$g_0 = \rho_W m_W \beta_1$	Parameter [1)]
$\rho_W = \rho_S/2$	Wood density as carbon (kg C m^{-3})
$\beta_1 = \beta_0(\beta_B + \beta_S)$	Parameter
$\beta_2 = \beta_0 - \beta_1$	Parameter
$\beta_0 = W_{SAP,T} / W_{SAP,A}$	The ratio of total sapwood $W_{SAP,T}$ to above-ground sapwood $W_{SAP,A}$ (kg kg^{-1}) [2)]
$\beta_B = h_B/L_C$	Parameter, where h_B is mean branch length ($C_W/2$)
$\rho_F = W_F/A_C$	Ratio of foliage mass to cross-sectional area of sapwood (kg C m^{-2})
$\rho_R = W_{FR}/A_C$	Ratio of fine root mass to cross-sectional area of sapwood, kg C m^{-2}
$s_0 = GPP/W_F$	Specific rate of photosynthesis kg C (kg C)$^{-1}$ year^{-1}

[1)] The maintenance respiration rates, m_i (Study III), for different biomass components (i=*F,R,W*, where *F*=foliage, *R*=fine roots, and *W*=sapwood in stem, branches, and roots) were needed in the g_i equations. The total maintenance respiration, R_M (kg C ha^{-1} yr^{-1}), was estimated based on the NPP:GPP ratio, r_{NPP}, as $R_M = R_T - R_G$, where R_G is proportional to NPP with fraction c (see Table A.1) as $R_G = c\ r_{NPP}$ GPP. The NPP:GPP ratio was estimated as r_{NPP} = 0.6 – 0.0113 H_{mean} (see Study II). As the rates for different components were unknown, the m_i:s were derived based on the relationships of rates $m_{i,0}$ introduced by Valentine and Mäkelä (2005) (see Table A.1) by scaling the maintenance respiration $R_M = m_F W_F + m_R W_{FR} + m_W (W_S + W_B + 0.5 W_{CR})$ to match the maintenance respiration estimated based on the NPP:GPP ratio. [2)] The proportion of sapwood was assumed to be 100% in branches and 50% in the coarse roots. Stem sapwood was calculated as $W_{SAP} = \rho_S (H_C A_C + (\varphi_C L_C A_C)$.

Appendix 2.

Appendix 2 contains the updated tables (A.4-A.8) of the RMSE, bias and standard deviation (absolute and relative values) of the estimation error (Study I) of stand basal area (m^2 ha^{-1}), basal-area-weighted mean diameter (cm), basal-area-weighted mean height (m), stand volume (m^3 ha^{-1}) in the end of the simulation period (1995), and growth of the stand basal area (m^2 ha^{-1} 10-years^{-1}) with n=597. These tables replace the Table 2 in Study I, as it included erroneously sample plots which had been thinned. Mark "**" indicate that the bias is significant (p<0.01) (based on the two-tailed paired samples t-test).

Table A.4. RMSE, bias and standard deviation (absolute and relative values) of the estimation error in plot level (n=597).

	Tree			Stand			Combined		
All (n=597)	**Abs**	**%**		**Abs**	**%**		**Abs**	**%**	
RMSE (abs. and %)									
Basal area (m^2 ha^{-1})	3.2	14.9		2.7	12.5		4.3	19.8	
Diameter (cm)	1.0	5.3		1.1	5.9		1.6	8.1	
Height (m)	1.7	11.7		1.8	12.1		1.8	12.4	
Volume (m^3 ha^{-1})	29.4	17.6		36.2	21.7		40.9	24.4	
Basal area growth (m^2 ha^{-1} 10-years^{-1})	3.2	59.5		2.7	50.0		4.3	79.2	
Bias (abs. and %)									
Basal area (m^2 ha^{-1})	0.1	0.6		0.7	3.2	**	1.0	4.5	**
Diameter (cm)	0.2	0.8	**	0.3	1.7	**	0.0	0.1	
Height (m)	0.7	4.4	**	0.8	5.4	**	0.7	4.6	**
Volume (m^3 ha^{-1})	7.3	4.4	**	1.7	1.0		3.9	2.3	
Basal area growth (m^2 ha^{-1} 10-years^{-1})	0.1	2.5		0.7	12.9	**	1.0	18.1	**
s (abs. and %)									
Basal area (m^2 ha^{-1})	3.2	14.9		2.6	12.1		4.2	19.3	
Diameter (cm)	1.0	5.3		1.1	5.6		1.6	8.1	
Height (m)	1.6	10.8		1.6	10.8		1.7	11.4	
Volume (m^3 ha^{-1})	28.4	17.0		36.2	21.6		40.7	24.3	
Basal area growth (m^2 ha^{-1} 10-years^{-1})	3.2	59.4		2.6	48.3		4.2	77.1	

** The bias is significant (p<0.01), based on the two-tailed paired samples t-test.

Table A.5. RMSE, bias and standard deviation (absolute and relative values) of the estimation error in Scots pine strata.

Scots pine (n=477)	Tree Abs	%		Stand Abs	%		Combined Abs	%	
RMSE (abs. and %)									
Basal area (m^2 ha^{-1})	2.3	19.5		2.1	17.3		2.3	19.3	
Diameter (cm)	1.7	8.5		1.8	9.0		1.7	8.6	
Height (m)	2.0	14.2		2.1	14.6		2.0	14.3	
Volume (m^3 ha^{-1})	20.1	23.2		22.0	25.4		22.6	26.0	
Bias (abs. and %)									
Basal area (m^2 ha^{-1})	0.2	1.5		0.8	6.5	**	0.4	3.6	**
Diameter (cm)	0.3	1.7	**	0.6	2.8	**	0.4	2.0	**
Height (m)	0.0	0.3		0.4	2.7	**	0.2	1.5	
Volume (m^3 ha^{-1})	2.7	3.1	**	6.2	7.2	**	4.4	5.1	**
s (abs. and %)									
Basal area (m^2 ha^{-1})	2.3	19.5		1.9	16.0		2.3	19.0	
Diameter (cm)	1.6	8.3		1.7	8.5		1.7	8.4	
Height (m)	2.0	14.2		2.0	14.3		2.0	14.2	
Volume (m^3 ha^{-1})	19.9	23.0		21.1	24.3		22.2	25.5	

Table A.6. RMSE, bias and standard deviation (absolute and relative values) of the estimation error in Norway spruce strata.

Norway spruce (n=389)	Tree Abs	%		Stand Abs	%		Combined Abs	%	
RMSE (abs. and %)									
Basal area (m^2 ha^{-1})	2.4	17.9		1.8	13.7		2.1	15.4	
Diameter (cm)	1.6	8.5		1.3	6.7		1.5	7.8	
Height (m)	2.3	15.2		2.5	16.4		2.4	15.7	
Volume (m^3 ha^{-1})	22.3	20.1		29.9	26.9		29.5	26.6	
Bias (abs. and %)									
Basal area (m^2 ha^{-1})	-0.7	-5.0	**	0.0	0.2		-0.4	-3.2	**
Diameter (cm)	-0.2	-1.0		0.0	-0.1		-0.2	-0.8	
Height (m)	1.1	7.5	**	1.5	9.6	**	1.3	8.6	**
Volume (m^3 ha^{-1})	1.9	1.7		-5.9	-5.3	**	-9.7	-8.7	**
s (abs. and %)									
Basal area (m^2 ha^{-1})	2.3	17.2		1.8	13.7		2.0	15.1	
Diameter (cm)	1.6	8.4		1.3	6.7		1.5	7.8	
Height (m)	2.0	13.1		2.0	13.2		2.0	13.1	
Volume (m^3 ha^{-1})	22.3	20.1		29.3	26.4		27.8	25.1	

Table A.7. RMSE, bias and standard deviation (absolute and relative values) of the estimation error in Silver birch strata.

Silver birch (n=110)	Tree Abs	%		Stand Abs	%		Combined Abs	%	
RMSE (abs. and %)									
Basal area ($m^2 ha^{-1}$)	0.8	24.0		0.9	28.3		0.9	26.4	
Diameter (cm)	3.5	18.4		4.1	21.0		3.7	19.0	
Height (m)	4.0	22.2		4.0	22.1		3.9	22.1	
Volume ($m^3 ha^{-1}$)	11.5	37.2		13.0	42.2		10.0	32.6	
Bias (abs. and %)									
Basal area ($m^2 ha^{-1}$)	0.2	6.4	**	-0.3	-9.7	**	0.0	0.6	
Diameter (cm)	0.1	0.5		-1.4	-7.3	**	-0.7	-3.5	
Height (m)	0.8	4.7		0.8	4.4		0.8	4.5	
Volume ($m^3 ha^{-1}$)	1.7	5.5		0.1	0.3		2.7	8.7	**
s (abs. and %)									
Basal area ($m^2 ha^{-1}$)	0.8	23.2		0.9	26.6		0.9	26.4	
Diameter (cm)	3.5	18.4		3.8	19.7		3.6	18.7	
Height (m)	3.9	21.7		3.9	21.6		3.9	21.6	
Volume ($m^3 ha^{-1}$)	11.3	36.8		13.0	42.1		9.7	31.4	

Table A.8. RMSE, bias and standard deviation (absolute and relative values) of the estimation error in White birch strata.

White birch (n=322)	Tree Abs	%		Stand Abs	%		Combined Abs	%	
RMSE (abs. and %)									
Basal area ($m^2 ha^{-1}$)	1.6	35.3		1.2	26.7		4.3	96.3	
Diameter (cm)	1.6	11.9		1.5	10.9		1.5	10.9	
Height (m)	2.2	16.2		2.2	16.0		2.2	15.9	
Volume ($m^3 ha^{-1}$)	11.7	38.6		10.1	33.6		29.9	99.0	
Bias (abs. and %)									
Basal area ($m^2 ha^{-1}$)	0.5	11.5	**	0.2	3.7		1.4	30.9	**
Diameter (cm)	-0.4	-3.1	**	0.1	0.9		-0.2	-1.6	**
Height (m)	1.0	7.5	**	0.9	6.4	**	0.9	6.8	**
Volume ($m^3 ha^{-1}$)	4.7	15.7	**	0.8	2.7		9.1	30.1	**
s (abs. and %)									
Basal area ($m^2 ha^{-1}$)	1.5	33.3		1.2	26.4		4.1	91.1	
Diameter (cm)	1.5	11.5		1.4	10.8		1.4	10.8	
Height (m)	1.9	14.4		2.0	14.7		2.0	14.4	
Volume ($m^3 ha^{-1}$)	10.7	35.3		10.1	33.5		28.5	94.3	