Dissertationes Forestales 11

Carbon stocks and flows in forest ecosystems based on forest inventory data

Aleksi Lehtonen

Finnish Forest Research Institute

Vantaa Research Center

Academic dissertation

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Author: Aleksi Lehtonen

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Supervisors: Prof. Annikki Mäkelä Department of Forest Ecology, University of Helsinki, Finland

Dr. Raisa Mäkipää Finnish Forest Research Institute, Helsinki, Finland

Pre-Examiners: Prof. Seppo Kellomäki Faculty of Forestry, University of Joensuu, Finland

Dr. Christian Wirth Max Planck Institute, Jena, Germany

Opponent: Dr. Robert A. Monserud USDA, Forest Service, Portland, OR, USA

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ABSTRACT

Countries are currently reporting changes in carbon pools of forests to UNFCCC. According to the reporting guidelines methods should be transparent and verifiable, and also the quantification of the uncertainty is asked.

The objective of the thesis was to develop methods for quantifying carbon stocks and fluxes at national scale based on forest inventory data.

To estimate tree biomass of forests, representative BEFs (biomass expansion factors) with uncertainty estimate were developed for Finland. A method for quantifying carbon flux of branches to soil was also developed. Both biomass and branch litterfall estimates were tested against independent measurements. Biomass estimation method and litterfall estimates were applied with Finnish forest inventory data to estimate carbon stocks and their changes for Finnish forests for 1922-2004. In this application main sources of litter were quantified based on forest inventory data and fed into dynamic soil decomposition model in order to estimate soil carbon stocks and its changes.

Application of BEFs, litterfall estimates and soil model gave time series of carbon stocks in Finnish forests. Results showed that tree carbon stock of Finland increased from 510 Tg to 780 Tg, while carbon in mineral soils increased from 850 Tg to 960 Tg during 80 year period. It was also found that there were high inter annual variation with soil- and tree carbon stocks caused by harvestings and temperature. According to the results, the NPP (net primary production) of Finnish forests has increased from 0.3 to 0.4 kg m⁻² during studied period, while NBP (net biome production) was positive since 1970s.

Results emphasize the importance of complete counting of changes of forest carbon pools i.e., trees, litter, soil and dead wood. Completeness will be important especially if forest management is used as a tool to mitigate climate change by enhancing carbon sinks of forests.

Keywords: BEF, carbon, biomass, litter, soil, forest inventory, greenhouse gas inventory

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Vantaa, October 2005

Aleksi Lehtonen

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by 5 research articles and one manuscript. These papers are reproduced with the permission of the journals in question.

- I **Lehtonen, A.**, Mäkipää, R., Heikkinen, J., Sievänen, R. & Liski, J. 2004. Biomass expansion factors (BEF) for Scots pine, Norway spruce and birch according to stand age for boreal forests. Forest Ecology and Management 188: 211–224.
- II Jalkanen, A., Mäkipää, R., Ståhl, G., Lehtonen, A. & Petersson, H. Estimation of biomass stock of trees in Sweden: comparison of biomass equations and age-dependent biomass expansion factors. Annals of Forest Science 62: (in press).
- III Lehtonen, A. 2005. Estimating foliage biomass for Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies (L.) Karst.) plots. Tree Physiology 25(7): 803–811.
- IV Lehtonen, A., Sievänen, R., Mäkelä, A., Mäkipää, R., Korhonen, K.T. & Hokkanen, T. 2004. Potential litterfall of Scots pine branches in southern Finland. Ecological Modelling 180(3): 305–315.
- V Muukkonen, P. & Lehtonen, A. 2004. Needle and branch biomass turnover rates of Norway spruce (Picea abies). Canadian Journal of Forest Research 34: 2517–2527.
- VI Liski, J., Lehtonen, A., Palosuo, T., Peltoniemi, M., Eggers, T., Muukkonen, P. & Mäkipää, R. Carbon sink of the Finnish forests 1922–2004 estimated by combining forest inventory data with modeling of biomass, litter and soil. (submitted manuscript)

AUTHOR'S CONTRIBUTION

I am fully responsible for the summary part of this doctoral thesis. I was responsible for the analyses and for most of the writing in I; for part of the writing and for partial design of the analysis in II; for all the writing and analyses in III; for all the analyses, and most of the writing in IV; for part of the writing and analyses concerning branch litterfall modelling in V and for analyses concerning biomass and litter estimation in VI.

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ABBREVIATIONS

А	years	Stand age
A _{cb}	$m^2 ha^{-1}$	Crown base basal area
BEF	Mg m ⁻³	Biomass expansion factor
С	kg C m ⁻²	Carbon stock
CO ₂	Tg	Carbon dioxide
dbh	cm	Diameter at breast height
F	kg C m ⁻² y ⁻¹	Fellings
G	$m^{-2} ha^{-1}$	Basal area
GHG		Greenhouse gas
ha	10000 m ²	Hectare
IPCC		International Panel on Climate Change
L	kg C m ⁻² y ⁻¹	Litterfall from vegetation
LULUCF		Land-use and Land-use Change and Forestry
Μ	kg C m ⁻² y ⁻¹	Annual natural mortality of trees
n	trees ha-1	Stocking density of a stand
NBP	kg C m ⁻² y ⁻¹	Net biome production
NEP	kg C m ⁻² y ⁻¹	Net ecosystem production
NFI		National forest inventory
NPP	kg C m ⁻² y ⁻¹	Net primary production
RE	kg C m ⁻² y ⁻¹	Roundwood removed from the ecosystems
R _h	kg C m ⁻² y ⁻¹	Heterotrophic respiration
RSE	%	Relative standard error
UNFCCC		United Nations Framework Convention on Climate Change
W_{f}	Mg ha ⁻¹	Foliage biomass

INTRODUCTION

Forests in the global carbon cycle

Circulation of carbon

Carbon circulates among the oceans, terrestrial biosphere and atmosphere. In addition, human activities, such as fuel combustion and deforestation, affect the carbon dioxide (CO_2) concentration of the atmosphere (IPCC 2001, Grace 2004). Growing trees and other vegetation capture CO_2 from the atmosphere and combine it with water, further producing sugars and carbohydrates. Meanwhile, it has been assumed that mature forests act as a carbon stock in which net exchange is close to nil, although this assumption has been questioned recently (Carey et al. 2001, Pregitzer and Euskirchen 2004).

The concentration of atmospheric CO_2 has increased from 352 ppm to 367 ppm during the 1990s (IPCC 2001 p. 208). Without terrestrial and oceanic carbon sinks the CO_2 concentration due to the amount of fossil fuels burned could have been 382 ppm during the late 1990s (IPCC 2001 p. 208). It has been estimated that approximately half of this total carbon sink originates from the land ecosystems of the earth and that the major part of this sink is located within forests in the northern latitudes (White et al. 2000, IPCC 2001 p. 213).

Role of forests in greenhouse gas mitigation

Quantification of forests as carbon sinks has been a challenge, and these estimates involve high degrees of uncertainty (Grace 2004) and discrepancies between methods (Houghton 2003). Estimation of the carbon budget of tree biomass based on consistent inventories (FAO 2001 p. 17) has been applied. However, other components of forest ecosystem carbon budget, such as heterotrophic respiration, loggings, other disturbances, soil processes and litter production, complicate the picture and uncertainty inherent in the carbon budget heavily increase (Kauppi et al. 1995, Schulze et al. 2000, Liski et al. 2002, Randerson et al. 2002).

The terrestrial sink amounted to 1.9 Pg of carbon annually in the 1980s, while carbon source due to deforestation was 1.7 Pg of carbon annually (IPCC 2001 p. 190). These estimates are based on various studies and models. House et al. (2003) compared various sources of information concerning terrestrial carbon sinks and concludes that extratropical regions have generally acted as net carbon sinks, although estimates between studies vary. Houghton (2003) suggested that the various sink estimates obtained with different methods were not due to high levels of uncertainty, but simply to incomplete counting of pools.

Emissions from fuel burning were about 5.4 Pg of carbon annually in the 1980s, therefore stopping deforestation and enhancing forest management practises that favour carbon sinks will not alone reduce the concentration of carbon in the atmosphere. The lower concentrations of CO_2 could be attained only by reducing emissions, but forest management could be used as a complementary tool to slow down the increase of CO_2 in atmosphere (Malhi et al. 2002).

The role of forests as carbon sinks can be much more important regionally than globally. A study by Monni et al. (2005) lists emissions and sinks of CO_2 by sources for Finland in 1990 and 2002. The carbon sinks of forests and soils were about 50 Tg of CO_2 , while emissions from fuel combustion were less than 60 Tg of CO_2 in 1990. Similar estimates for 2002 were about 10 and 65 Tg of CO_2 for forests as sinks and emissions from fuel combustion, respectively. During both years the soil carbon stock change of mineral soils could have been either sink or source, due to degrees of large uncertainty. The study by

Monni et al. (2005) also indicates the importance of interannual variation and the high level of uncertainty of soil sinks.

Greenhouse gas reporting

Clear indication of the importance of the terrestrial biosphere as a part of the global carbon budget has been acknowledged, and inclusion of carbon sinks in greenhouse gas inventories was decided in Rio de Janeiro in 1992 by the UNFCCC (United Nations Framework Convention on Climate Change). The Kyoto Protocol of the UNFCCC was a first step towards limiting emissions of CO_2 and other GHGs. It was also agreed in Kyoto that sinks can be used to compensate emission reductions. The Conference of Parties (COP7), referred to as the Marrakesh Accords, invited IPCC to develop guidelines for GHG inventories in the LULUCF (Land use, and Land-use Change and Forestry) sector. These guidelines (IPCC 2003) give instructions for GHG inventories in the LULUCF sector concerning the methods, default values and pools to be covered. Five forest carbon pools should be covered by inventory, namely aboveground and belowground biomass, coarse woody debris, litter and soil organic matter (IPCC 2003). All these pools should be quantified, unless it can be shown that a pool is not a source of carbon.

Previously, national reporting of LULUCF sector to the UNFCCC has relied on biomass estimates of trees, excluding other carbon pools such as soil, litter and coarse woody debris. Countries have widely used the default method, in which the stem volume increment minus losses (drain) was converted to net carbon stock change with simple conversion factors (Löwe et al. 2000, Tomppo 2000, UN-ECE/FAO 2000 p. 155).

Currently, countries are improving their national GHG inventories to be able to fulfil the reporting requirements set by the new guidelines (IPCC 2003) and methodological developments and options are being discussed (Ståhl et al. 2004). The most challenging carbon stock changes to quantify are apparently changes in coarse woody debris, litter and soil organic matter.

Methods to assess carbon flows of forests

Currently, forest carbon budget is studied with various techniques such as process-based models, CO₂ flux measurements by eddy covariance technique, remote sensing and the forest inventory-based approach (Houghton 2003, Grace 2004, Lindner et al. 2004). There is a strong tradition of ecological research that has quantified various fluxes of carbon and nutrients at the stand-level (Viro 1955, Mälkönen 1974, 1977, Helmisaari et al. 2002). In addition, field stations have stands that have been extensively studied for decades. Many process-based models have been parameterized with data obtained from these stands (Mäkelä and Hari 1986, Running and Coughlan 1988, Hari et al. 1990, Kellomäki et al. 1992, Hari et al. 1996). These models give insight into the underlying processes and enhance their understanding, typically by including all the major processes and fluxes that can be quantified. The disadvantage of these models is often the limited applicability, i.e. when very site-specific they do not apply very well to other conditions (Kramer et al. 2002). In addition, many of these models are problematic during modelling of soil processes. The advantage to have these different approaches is that methods can be used to compare results and assumptions of various models and empirical data.

These process-based models received an additional source of information and testing material when the eddy covariance method was established. This method assesses the net exchange of carbon between Earth and the atmosphere by measuring CO_2 concentrations and air turbulence (Baldocchi 2003). The advantages of this method are its high resolution over time and direct measurement of net change, while the disadvantages include uncertainty in determination of source area, difficulties with night-time fluxes and very site-specific measurements.

Remote sensing can be used with process-based models to quantify the net primary production of forests (NPP) (Myneni et al. 2001, Nemani et al. 2003). The advantage of this approach is that it can cover large areas with a uniform method, while the disadvantages are that it indirectly measures carbon and is not able to quantify the understorey or belowground biomasses. On the other hand, this method requires extensive ground surveys to calibrate reflectance values from images with actual biomass and/or NPP. Moreover, this method relies on the parameterization of models based on a few sites, but can thereafter be applied over a wide gradient of conditions.

Forest inventory-based approaches to estimate carbon stocks and flows use the NFI (national forest inventory) or other sampling networks that cover a wide range of conditions across a country or region. The output variables of traditional forest inventories are forest area and stem volume, and the latter is then converted to biomass and carbon. If other pools in addition to carbon of living biomass are to be quantified, then turnover rates can be applied to estimate the litter flux to soil (Kurz and Apps 1999, Liski et al. 2002). The flux of understorey vegetation litter to soil should also be quantified. After estimating all litterfall components, one can estimate the changes in soil carbon stock through the soil model. The concepts of inventory-based approach that cover all these 5 carbon pools specified by IPCC (2003) were presented by Kurz and Apps (1999) and more recently by Liski et al. (2002).

Empirical studies on biomass have focused on quantifying these pools, either for energy use or to study nutrient cycling. The life span of biomass components is less known, especially that of belowground pools. The life span and longevity of foliage was studied to evaluate different strategies of species (Westoby et al. 2002), and to examine the responses to changing environment and pollution (Jalkanen et al. 1981, Jalkanen et al. 1998). These estimates of needle life span are often needed as an input variable in process models (Bassow et al. 1990, Osborne and Beerling 2002). Moreover, the average life span of foliage is not enough for estimation of the turnover rate of foliage biomass, because biomass of shed needles is lower than that of green needles due to nutrient reuse (Viro 1955) and because the needles are partially shed from younger cohorts as well (Muukkonen 2005). Therefore, the inverse of the mean life span of foliage is not an appropriate estimate for needle turnover in terms of biomass (Muukkonen 2005). The life span, death and growth patterns of branches were examined to maximize wood quality (Kellomäki and Tuimala 1981, Madgwick et al. 1986, Kellomäki and Väisanen 1988, Maguire 1994, Mäkinen 1999, Mäkinen and Colin 1999, Ishii et al. 2000, Mäkinen et al. 2002, Mäkela and Mäkinen 2003, Mäkinen et al. 2003). However, very little is known of the litterfall of large branches, except for the few studies that have proposed alternative approaches, such as branch mortality dating by Maguire (1994). Knowledge of the fine root turnover of tree species in Finland relies on a rather limited number of studies (Majdi 2001, Helmisaari et al. 2002, Cronan 2003, Ostonen 2003, Majdi and Andersson), that reported similar values for turnover varying from several months to two years. Recently, however these estimates for fine root turnover have been challenged by studies using isotope tracers, such as those by Matamala et al. (2003) and Gaudinski et al. (2001), who reported turnover rates up to 8 years for fine roots.

Repeated soil carbon measurements often do not exist and therefore soil processes and carbon stocks changes have been studied mostly through the use of decomposition models (Ågren et al. 1991, Chertov and Komarov 1997, Kurz and Apps 1999, Wang et al. 2001, Liski et al. 2005). Sweden is a rare example of a country with a repetitive sample of soil carbon measurements that is available for carbon stock change estimation (Ståhl et al. 2004).

Dynamics of tree- and stand level biomass

Traditionally, monitoring of forest resources has focused on estimation of stem volume to quantify wood resources for the forest industry. Other biomass components of trees, in addition to stem, were studied more intensively when increasing interest was shown in biomass as an energy source (Hakkila 1989). During that time extensive biomass samplings were carried out in Scandinavia (Marklund 1988, Hakkila 1991). In addition to biomass modelling, there has been a strong tradition in quantifying carbon and nutrient flows at single sites. These studies have measured all the different biomass pools and their nutrient concentrations (Viro 1955, Mälkönen 1974, 1977, Oren et al. 2001, Helmisaari et al. 2002, Cronan 2003, Ostonen 2003).

Biomass proportions of trees

Theories on the allocation rules of carbohydrates can be used for quantifying biomass of trees at various scales, e.g. tree, stand and region. These rules were discussed thoroughly by Mäkelä (1990) and by Lacointe (2000), concluding that the partitioning of carbohydrates for tree growth of different biomass pools and their respiration is not adequately known. Some structural relationships of tree species, such as functional balance and the pipe model theory appear to hold and be applicable when the biomass proportions of trees are modelled.

The concept of optimality (Hari et al. 1990) states that trees allocate carbohydrates in such way that they maximize annual photosynthesis with the constraining carbohydrate amount. Assuming that the concept of optimality holds leads to the assumption that both functional balance and the pipe model theory link the structure and function of the biomass components of trees.

The functional balance theory (Davidson 1969) states that plants balance between shoot and root biomass. This theory underlines the correlation between the nitrogen uptake of roots and carbon assimilation of foliage. The basis of the theory according to Davidson (1969) is that the carbon and nitrogen are used at a constant ratio and that the assimilation of carbon and nitrogen must be in balance with this use.

The pipe model theory was proposed by Shinozaki et al. (1964), they claimed that the sapwood area at a certain height is proportional to the foliage biomass above that height. This theory has been widely applied and further developed. Mäkelä (1990) showed that the total sapwood area of primary branches also correlates with tree foliage. These dependencies are often used in models that describe canopy structure and its function (Mäkelä and Vanninen 2001).

In addition to maintaining the root-shoot relationship and the relationship between sapwood area and foliage, trees also prioritize carbohydrate allocation. Oliver and Larson (1996 p. 75) described that priority of carbohydrate allocation is given to maintenance respiration, which is followed by fine root and foliage production, flowering, height growth and diameter growth, although recognizing that the order of the priority may change temporarily.

Assuming that the concept of optimality, theories of functional balance, pipe model approach and priority of allocations hold leads to the assumption that the biomass proportions of single trees is dependent on various environmental conditions, genetics and also on tree age. These environmental conditions and their interactions have been tested in numerous studies, e.g. for fertility (Vanninen and Mäkelä 1999), radiation, CO_2 fertilization (Oren et al. 2001), competition (Mäkelä and Vanninen 1998, Naidu et al. 1998, Vanninen and Mäkelä 2000), silviculture and tree age (Vanninen et al. 1996, Cairns et al. 1997).

Stand-level biomass proportions

Stand-level biomass is an aggregation of single-tree biomasses. Destructive biomass measurements are conducted at the tree-level and the selection of sample trees is done based on certain criteria. Biomass measurements at the stand-level do not really exist and therefore up-scaling from tree to stand-level is needed. When this up-scaling is done one must assume that the biomass of a sample tree represents well the biomass of a stand.

A pool of resources is available for the vegetation at the stand-level, and an individual tree acquires resources according to its competitive status among other trees, while the sum of resources at the stand-level is rather constant, affected by use or by external input. In growth and yield studies the productivity of a site is measured by the dominant height that has been achieved at a certain stand age. This variable describes the fertility of soil and also the ability of trees to transport water to the canopy. This relationship of height and stand age aggregates a wide range of effects that influence the growth of trees (Assmann 1970 p. 44) and reflect the overall resources of a site.

In various process models the relative proportion of biomass components changes after canopy closure (Berninger and Nikinmaa 1997), which is the time point when light conditions change drastically (Oliver and Larson 1996 p. 79). The relative proportion of foliage biomass later decreases, while the relative biomass of stems continues to increase (Satoo and Madgwick 1982 p. 51). Moreover, the quantity of living cells in a tree is so large at later points, that increased amounts of carbohydrates must be made available for maintenance respiration (Oliver and Larson 1996 p. 78, Mäkelä and Valentine 2001), while less is available for foliage, fine root and height growth. Thus, sites with similar production capacities differ in biomass proportions, especially if they are at different developmental phases or have very different soil properties and/or climatic conditions (e.g. temperature and radiation).

The variation of trees allometry between sites is dependent on the fertility, soil properties, radiation, silviculture and stand age. Here the allometry is defined as structural dimensions of trees, including various measures, like distances and mass relationships. Stand biomass sums up the biomass of individual trees, and thereafter the information by individual trees is lost. Assuming an even-aged structure of a single tree species that has been often the target of forest management, one can summarize that the biomass proportions at the stand-level are dependent on various environmental factors, stand age and genetics of those trees.

Based on these assumptions that genetics drives the allometry of trees species (especially in boreal zone and with trees having similar growing conditions) (Kramer and Kozlowski 1979 p. 70), and based on the assumptions that tree age affects the relative proportions of biomass components (foliage, branches, stem and roots) (Oliver and Larson 1996 p. 79) we derived a conversion factors for biomass, namely BEFs. These biomass expansion factors were modelled by tree species, biomass component and as a function of stand age, in order to account the variation within relative proportions of biomass components by age. The BEF here was defined as a ratio between biomass and stem volume.

Senescence of biomass compartments

The carbon balance theory states that increment biomass equals growth minus senescence (Mäkelä 1990). In other words, what goes up must come down; only the time span varies. The mean life span of different biomass components, such as foliage, fine roots, branches and coarse roots, varies depending on the function of the component.

The life span of fine roots is lowest among tree biomass components. Field et al. (1992) showed that fine roots die when roots expand to explore new regions in soils. Thus, senescence of fine roots is dependent on the growth rate of trees and their ability to reuse nutrients (Field et al. 1992). Helmisaari et al. (2002) found that the proportion of annual production of fine roots increased with stand age, indicating that older trees may have higher senescence rates of fine roots. Mäkelä (1988) derived senescence rates for fine roots of Scots pine in soils with different fertility by combining the pipe model theory and assumptions of functional balance. She concluded that fine roots have higher turnover rate with unfertile sites. Although, this may hold under optimal site conditions, additional nutrient fertilization may thereafter decrease the carbohydrate allocation to fine roots. On the other hand Majdi and Andersson found that fertilization increased fine root biomass and production within a nutrient-limited Norway spruce site.

The life span of foliage is dependent on climatic conditions (Kouki and Hokkanen 1992, Muukkonen 2005, Starr et al. 2005), nutrients (Schoettle and Fahey 1994) and on photosynthetic efficiency (Westoby et al. 2002). The life span of foliage appears to vary between species, depending on their ecological strategy (Warren and Adams 2000, Osborne and Beerling 2002, Westoby et al. 2002). As a needle cohort ages its photosynthetic production decreases (Kramer and Kozlowski 1979 p. 216) due to nutrient removals (Chabot and Hicks 1982) and self-shading, the net carbon gains decreases (Chabot and Hicks 1982) and eventually needles are shed.

Supportive structures of trees, such as branches, coarse roots and stems have longer life spans compared with those of foliage. However, branches die due to shading and crown rise, while much less is known of the senescence of coarse roots, which is often assumed to be equal to that of branches (e.g. Liski et al. 2002). Moreover, branch litterfall appears to be more of a random phenomenon that is dependent on stochastic variables such as strong winds, while stems accumulate, and form dead cells referred to as heartwood, which will eventually form litter input to the soil, after the tree has died and collapsed.

Soil carbon and it's changes

Soil carbon stocks are built up during time spans of tens of thousands years. In Finland organic layers of soils mainly started to accumulate after the glacial period about 10 000 years ago. The vegetation produces organic matter (by litter and mortality), which is thereafter decomposed by soil flora and fauna. Small fractions of this organic matter are left to accumulate and form more permanent carbon compounds. Inert carbon forms are also stored in soils during forest fires.

Soil carbon stocks and the changes that occur in them are the results of climate, soil properties, litter quality and litter production by vegetation; the more productive the site is the more litter is fed into soil (Schimel et al. 1994, Liski and Westman 1997). Tamminen

(1991) also found an increasing trend in soil carbon according to site type, indicating that more fertile soils had more carbon.

Organic matter that is fed into soil originates from vegetation and soil microbes, which constitutes mainly carbohydrates, lignin, nitrogen compounds, fats and minerals, The decomposition of organic matter in boreal soils is mainly driven by temperature (Mikola 1960, Kirschbaum 1994, Liski and Westman 1997, Liski et al. 2005), while also nutrient availability and drought has impacts to the decomposition (Berg and Matzner 1997). On the other hand Peltoniemi et al. (2004) concluded based on simulations and measurements that soil carbon stocks were higher in the warmer conditions that indicates higher impact of temperature to litter production compared to that of decomposition.

Different chemical compounds included in the litter have different decomposition rates and end products (Berg et al. 1982). Liski et al. (2005) grouped litter that was fed into soil according to dimensions and chemical compositions, the groups of litter were non-woody, fine woody and coarse woody litter. The dimensions of litter influences the decomposition rate, due to fact that larger logs take more time to be exposed to microbial community. The initial phase of decomposition is well known phenomena, e.g. when lignin, cellulose, hemicelluloses and extractives decompose, but the latter part of it is less known and harder to quantify and especially the formation mechanism of humus is poorly known (Berg and McClaugherty 2003 p. 16–30). The quantity and dynamics of litter production varies between tree species, which further influences soil carbon stocks (Palosuo et al. 2005). According to Peltoniemi et al. (2004) Norway spruce stands had more carbon in mineral soils compared to that of pine in mesic sites. Varying carbon stock by species is an important result and should be more studied especially when tree species composition might change due to warming of climate and due to changes in competitive advantages of species (Kellomäki and Kolström 1992).

Information requirements

Biomass estimation

The net change in the carbon stock of trees in Finland was reported by the Finnish Forest Research Institute to the UNFCCC according to guidelines of the IPCC (1996). Conversion of annual net increment of growing stock was done by simple expansion factors and wood density estimates by tree species (Karjalainen and Kellomäki 1996, Tomppo 2000). The disadvantage of this estimation method was that the source data and uncertainties of the expansion factors were not known.

Biomass estimation methods are also available at the tree-level (Marklund 1988, Hakkila 1991), but so far these have not been used in the Finnish national GHG reporting schemes. In addition, stand-level or regional-level biomass estimation methods with uncertainty estimate, such as appropriate BEFs (biomass expansion factor), were lacking. Biomass estimations of increment and losses were needed due to fact that default method by the guidelines of the IPCC (2003) was chosen to be used in the Finnish GHG inventory (Tomppo 2000), and especially since the appropriate Finnish biomass equations do not exist (Kärkkäinen 2005). Thus a need became apparent for stand-level biomass estimation tools that can convert drain to biomass.

Tree allometry is species dependent and varies according to tree size and therefore the size distribution of trees and its changes should be known for adequate biomass change

estimation (Satoo and Madgwick 1982 p. 81, Lacointe 2000). Currently, forest inventory data are often available in aggregated form, where stem volumes are reported by species and age-classes. Thus, factors that convert stem volumes to total tree biomass were needed. In addition to changes in size distribution, the age distribution of forests also changes due to management operations resulting from forest policy instruments, and therefore conversion factors should be able to take this effect of altering age-class distribution into account when carbon pools and fluxes are quantified.

Estimation of changes in soil carbon stock

Soil carbon stock and its changes have been estimated by measurements, but the quantity of these changes has been extremely difficult to detect, due to relatively small changes of a large stock. Soil carbon content has high variation within sites and observations are correlated between each other within low distances (Liski 1995, Ståhl et al. 2004). Kauppi et al. (1997) used statistical models to correlate NFI measurements with soil carbon measurements. The advantage of this approach was the easy extrapolation based on the measurements of soils and trees. The disadvantage of these statistical models is that they lack historical development of soils and due to that major part of the variation if often unexplained.

To fulfil reporting needs (UNFCCC 1997, IPCC 2003), countries must develop methods that allow the estimation of carbon pools soil, litter and deadwood. These estimates should be relevant at national scales, and thus up-scaling should only be done based on appropriate sampling methods such as NFI. Since nation-wide soil surveys have not been done as extensively as forest inventories focused on trees dynamic soil models are needed to estimate the rates of change of the carbon pools in soil, litter and deadwood. Sweden seems to be a rare example with a large dataset of soil samples (ca. 3000 plots) with re-measurements available.

The solution for fulfilling the current information needs (IPCC 2003) by researchers in Finnish Forest Research Institute was to further develop the concepts of Kurz and Apps (1999) and Liski et al. (2002) to estimate the soil carbon stock and changes occurring in it. A combination of 9 consecutive NFIs, age-dependent BEFs, tested turnover rates and the dynamic soil model allowed us to estimate those pools that have been listed by the IPCC (2003).

Objective

The overall objective of this study was to develop methods for estimating carbon stocks and flows in forest ecosystems based on inventory data, especially litter input estimation to improve soil carbon estimation with the dynamic model.

The specific objectives here were:

- to improve regional biomass estimation methods by BEFs that take into account varying biomass proportions during stand development;
- to test our biomass estimation methods, especially that for foliage, for its importance in litterfall estimation;
- to develop estimates and models for branch litterfall to quantify this poorly known flux under conditions present in Finland, and to present a concept that describes the estimation of this flux;

- to estimate soil carbon stock changes in mineral soils with estimated litterfall, because estimates of this pool change do not exist but are meanwhile requested by the governmental officials;
- to describe carbon stocks and flows in Finland's forests from 1922 to 2004 by the methods developed.

MATERIAL AND METHODS

Material

Permanent sample plot data

The permanent sample plot data used in (I, IV, and V) were collected by Finnish NFI. The dataset consists of about 2300 sample plots on forest land, and measurements from 1985 to 1986 and 1995 were used. Sampling was denser in southern Finland, with clusters every 16 km, each with 4 plots separated by distances of 400 m. The distances in northern Finland between clusters were 24 km (south-north) and 32 km (east-west), each with 3 plots separated by the distances of 600 m. Sampling was described in detail by Mäkipää and Heikkinen (2003).

From each plot data were collected concerning the plot, each compartment and each tree. Plot- and compartment-specific data consisted of information on the stand such as location, site type, silviculture, stand age, topography, soil type, habitat data, land-use, etc. Tree-level data consists of observations of individual trees, where trees with dbh more than 10.5 cm were measured from plots having fixed radii of 9.77 m (300 m²); smaller trees were measured from a plot that had radii of 5.64 m (100 m²). These trees are mapped by species, location and dbh. Tally trees were measured from the same plot but with radii of 4.89 m. In addition to species, location and dbh, tally trees were measured for crown base height and tree height and also for various parameters that describe wood quality and crown properties.

The BEFs were estimated by combining tree-level data of these permanent sample plots measured in 1985–1986 with biomass and volume equations (Laasasenaho 1982, Marklund 1988) in order to estimate biomass and volume of each plot (I). Thereafter, plot-wise biomass and stem volume estimates were used to estimate BEFs, which were plotted by stand age and tree species.

Measurements from both 1985–1986 and 1995 were used, especially those concerning crown base height, to estimate the change in crown height during the period between measurements (IV, V). Data on tree dimensions (dbh) and stand density (stocking per hectare) were also used when potential branch litterfall was modelled.

National forest inventory

Finland

Aggregated NFI results were used of which growing stock and forest area data by species and age-classes were employed to estimate biomass and litter flux to soil (VI). In this study, forest resource information of all 9 NFIs excluding the 4th NFI, were used (Ilvessalo 1956, Kuusela 1972, 1978, Kuusela and Salminen 1991, Tomppo and Henttonen 1996, Hökkä et al. 2002, Tomppo et al. 2003, Tomppo et al. 2004).

Sweden

Both tree-level and aggregated NFI data of Sweden from 1997 to 2001 were used (Anon. 2002) in (II). The methodology and sampling in the Swedish NFI were described by Ranneby et al. (1987). The tree-level data contained diameter distributions for each sample plot, while aggregated stem volume data were also used, in which grouping was done by dominant species and stand age-classes. These stem volumes were used for aboveground biomass estimation of trees in Sweden for 4 regions (II), excluding mixed stands (less than 70% basal area with single species). Biomass was estimated using 3 different approaches: with tree-level data and biomass equations (Marklund 1988), aggregated stem volume data converted to biomass with BEFs (I) and finally with constant BEFs applied in Sweden's GHG inventory (Feldhusen et al. 2004).

Biomass measurements of the national tree research (VAPU)

The biomass data used in study were collected in 1988–1990 by national tree research project (VAPU) (III–V); the sampling and principles of data collection were described by Korhonen and Maltamo (1990). These plots were a sub sample of temporary plots from the 8th NFI, the dataset includes 195 Scots pine and 196 Norway spruce that were felled and measured for dimensions and each for aboveground biomass. A total of 3–6 sample trees (dbh more than 5 cm) were felled closest to each plot centre, depending on stand diversity (3 trees in monoculture and an additional 3 from mixed stands).

Stems of each sample tree were measured for diameter at various heights to estimate stem form. The foliage and branch biomasses were also sampled for these trees. On average 10 branches were measured for fresh weight, while 3 of these were taken to the laboratory for dry weight determination. All branches from each felled tree were measured for location and diameter, except with the larger Norway spruce (height more than 10 m), when every second metre from the canopy was measured.

In addition to felling of the sample trees, the other trees in a plot were also measured. The plot radius was the most distant felled tree plus 2 m, but at least 5 m. All trees from the plot were measured for location, species, dbh, height and height of the crown base. In addition to the biomass measurements, needle survival was also estimated from the felled trees. Two branches from the 15th whorl were selected and the percentage of needles left in each needle age cohort was estimated.

Litter measurement plots

The branch, foliage and flower litterfall have been collected from litter collection sites established on Scots pine and Norway spruce stands since the 1960s by the Finnish Forest Research Institute (Sarvas 1968, Kouki and Hokkanen 1992). The branch litterfall estimates obtained from models were compared with these measurements (IV, V). The branch litterfall for Scots pine was collected from 7 stands in southern and from 4 stands in northern Finland, while that for Norway spruce was collected from 4 sites in the south and 2 in the north (Tables 1 and 2).

Site	G	n	А	Branch litter	
	(m² ha-1)	(trees ha-1)	(years)	(kg ha ⁻¹)	
Kittilä 1*	11.2	204	250	30	
Kittilä 2*	22.7	408	220	69	
Rovaniemi 27*	24.6	364	140	85	
Rovaniemi 29*	15.8	174	136	100	
Eckerö 1	26.7	584	170	144	
Vilppula 2	24.6	237	223	199	
Kuorevesi 23	24.3	288	134	180	
Aulanko 29	19.4	587	57	78	
Punkaharju 45	23.8	260	149	133	
Noormarkku 86	29.2	580	116	144	
Heinola 567	13.7	136	157	142	

 Table 1. Description of branch litter collection sites for Scots pine, with basal area (G), stocking (n), stand age (A) in year 2000 and mean branch litterfall.

* Sites located in northern Finland

Table 2. Description of branch litter collection sites for Norway spruce, with basal area (G), stocking (n), stand age (A) in year 2000 and mean branch litterfall.

Site	G (m² ha ⁻¹)	n (trees ha ⁻¹)	A (years)	Branch litter (kg ha ⁻¹)
Kittilä 4*	23.7	528	202	166
Rovaniemi 18*	20.8	606	157	168
Aulanko 27	40.1	228	165	629
Heinola 565	32.8	313	147	381
Kuorevesi 35	27.7	590	140	236
Siilinjärvi 544	23.1	322	101	299

* Sites located in northern Finland

Methods

Models for BEFs

It is well known that the fraction of canopy and root biomass decreases during stand development (Assmann 1970 p. 38, Satoo and Madgwick 1982 p. 51, Oliver and Larson 1996 p. 51). This is because stem growth is completely preserved during heartwood formation whereas the other compartments such as foliage, branches and roots turn over and are thus partly lost as litter. The quantity of foliage stabilizes at a certain level, while the woody components of trees continue to accumulate, especially after canopy closure. Since the relative proportions of biomass components such as roots, foliage and branches, change during tree development, BEFs (Mg m⁻³) were estimated as functions of stand age (I).

The BEF were estimated for all biomass components that had been modelled by Marklund (1988), as a function of dbh, see Eq. (1). Tree-level biomass and volume estimates calculated with the model (Laasasenaho 1982, Marklund 1988) were added up to plot level and the BEFs for biomass components were calculated by dividing stand level biomass estimates by

stem volume estimates see Eqs. (1, 2 and 3). Thereafter, the BEFs for total and aboveground biomass were also estimated for each plot, see Eq. (3). Biomass W by tree species j and by biomass component i was estimated also with power function, where a, b and c are parameters, while dbh is diameter at breast height (Marklund 1988).

$$W_{ij} = a_{ij} \times \left[\frac{dbh}{dbh + c_{ij}}\right]^{b_{ij}} \tag{1}$$

Stem volume V by species j was estimated with simple power function, where a and b were parameters that vary according to tree species j, while dbh is diameter at breast height (Laasasenaho 1982).

$$V_j = a_j \times dbh^{\nu_j} \tag{2}$$

In order to estimate BEF for each stand, biomass W was divided with stem volume V, and according to biomass component or those sum (i = foliage, branches, stem, dead branches, bark, stump, coarse roots, small roots, aboveground or whole tree) and by tree species j (I).

$$BEF_{ij} = \frac{W_{ij}}{V_j} \tag{3}$$

Plotwise BEF values were then modelled according to stand age for all biomass components (I). These models were estimated with the time-dependent term $e^{-0.01t}$, where t was time and e was the base of a natural logarithm, while a and b were parameters, see Eq. (4). The time t was modified to derive an optimal and logical fit for the BEF as a function of stand age.

$$BEF_{ii}(t) = a + b \times e^{-0.01 \times t} \tag{4}$$

Error estimation of BEFs

L.

The BEFs for total biomass and for aboveground biomass for broadleaved stands were also estimated using stand age-classes to estimate the relative standard error (RSE) of these BEFs according to age-class (I). The RSE includes sampling error of the NFI and model errors of the biomass (Marklund 1988) and volume equations (Laasasenaho 1982).

Correlation between errors of biomass components (e.g. branches and foliage) was assumed to be zero, for practical reasons, although it was shown by Dean and Cao (2003) and by Wirth et al. (2004) that these correlations do exist. To account for model error, both full correlation and zero correlation between errors at the cluster level were estimated. These 2 approaches enabled us to estimate the minimum and maximum RSEs for these age-classes.

Application of BEFs to Swedish NFI

The aboveground biomass for Sweden was estimated using 3 alternative methods: more precise estimation using the tree-level data and biomass equations of Marklund (1988), estimation with age-dependent BEFs (I) and estimation with the constant BEFs used in the Sweden's national inventory report by Feldhusen et al. (2004). Constant BEFs were applied to the aggregated NFI volume data by species, while age-dependent BEFs were used with stem volume estimates by age-classes to convert stem volumes to aboveground biomass (III).

The errors for biomass estimates using the tree-level approach and age-dependent BEFs were estimated. The RSE was estimated for the tree-level approach by combining the NFI sampling error and the biomass model error, while the RSE of the biomass estimate by age-dependent BEFs resulted from a combination of the RSEs of both the volume estimate and BEF. The uncertainty estimation of the BEFs is reported elsewhere in more detail (I).

Predicting foliage biomass from measurements

Biomass measurements of the VAPU database were used to test various foliage biomass estimation methods. The reference foliage biomass estimates were up-scaled from single branches to stand-level with a sequence of empirical models, trying to utilize various measurements of sample trees and plots. Branch observations from the same tree and also trees from the same plot were correlated, and therefore linear mixed models were applied (McCulloch and Searle 2000).

The fresh mass of branches was measured for an average from 10 branches per tree, while dry mass and needle mass were measured from 3 branches per tree. The first mixed model was then estimated for the relative proportion of foliage in each branch, incorporating data on branch diameter, branch location and tree size. The intercept and branch location were allowed to vary among trees, having zero as the expected value.

The foliage biomass estimate of each branch was then modelled using branch diameter and location, with varying intercepts and branch diameters at the tree-level. The basal area of the crown base of each tree from all plots was then predicted in a model using various predictors such as tree dimensions and height of crown base.

After finding the foliage biomass estimate for each sample tree and the estimated crown base basal area (A_{cb}) of each plot, foliage biomass was up-scaled to plot level. The up-scaling was done by modelling the foliage biomass (W_f) to crown base basal area (A_{cb}) ratio of each plot. This ratio was thereafter multiplied with estimates of plot-level A_{cb} . The predicted W_f estimates at the plot level (see above) were thereafter compared with estimates of W_f obtained with alternative methods.

Testing foliage biomass estimation methods

The W_f estimates were tested against alternative methods that varied by information needs and parameterization data (Table 3). First, W_f was estimated with the methods presented ealier (I), where the inputs were stem volume and stand age. Thereafter, the W_f was estimated using the more sophisticated approach presented by Valentine et al. (1994), which requires W_f : A_{cb} ratios, basal area and crown ratio. The biomass models of Hakkila (1991) and Marklund (1988) that require data on dbh, height and crown base height were also applied in this test.

	Method						
	Biomass estimation methods (I)		Valentine et al. (1994) approach		Biomass equations		
	(1) BEF	(2) Volume to biomass	(3) Valentine + crown ratio model	(4) Valentine	(5) Hakkila	(6) Marklund	(7) Biomass eqs. (III)
Stem volume	Y	Y					
Stand age	Y						
Stand basal area			Y	Y			
Stand average crown ratio				Y			
dbh at tree-level					Y	Y	Y
Height at tree-level					Y	Y	Y
Crown base height					Y		
Pipe model ratio for foliage			Y	Y			
Parameterization based on reference data			Y	Y			Y

Table 3. Alternative methods for foliage biomass estimation and their information requirements.

Models for potential branch litterfall

We combined empirical models of the vertical biomass distribution of branches and crown base height increase, to obtain an estimate of potential branch litterfall (IV, V). The biomass distribution model was based on the VAPU database, while the crown base height increase was derived from permanent sample plots of the NFI. The modelling approach is described elsewhere in more detail (IV, V).

A linear mixed model (McCulloch and Searle 2000) was used to model branch biomass as a function of branch diameter, with intercept and branch diameter varying between trees as random parameters. Thereafter, the vertical biomass distribution of branches was modelled with a polynomial function that had relative height and crown ratio as predictors. This model was then applied to data for permanent sample plots, from which consecutive measurements of crown base height can be obtained. This approach allowed the estimation of potential branch litterfall for Scots pine and Norway spruce in southern Finland.

Testing potential branch litterfall

Branch litter models (IV, V) were tested against litter trap measurements. The branch biomasses of these sites were modelled, based on tree-level data and the biomass equations of Marklund (1988), where dbh and tree height were used as predictors. Thereafter, models for potential branch litterfall (IV, V) were applied to estimate the relative litterfall for each tree. These models accounted for stand density and tree diameter (dbh). Constant turnover rates of 2.7% and 1.25% relative to branch biomass for Scots pine and Norway spruce sites were also applied. This allowed comparison of measured with predicted litterfall, based either on the model or on the constant turnover rate.

Models for needle litterfall

The needle shed dynamics of Norway spruce was analysed by using the VAPU dataset that included the measurements concerning needle survivor classes (V). The cumulative probability of needles living was modelled with ordinal regression over the needle survivorship classes. The data were modified by the mass loss factors derived from Viro (1955). The time needed to attain a cumulative probability of 50% was then estimated and the turnover rates for foliage were derived.

Calculation scheme of national carbon budget

The soil carbon stock and the changes occurring in it were estimated with the help of the Yasso soil carbon model (Liski et al. 2005), while the litter input to soil model was estimated from the tree and understorey biomasses based on NFIs and from drain statistics (Metla 2004 p. 71) (VI). This approach builds on the earlier works of Kurz and Apps (1999) and Liski et al. (2002), in which biomass estimates, litter production, disturbances and the soil decomposition model were integrated.

The aggregated NFI results on stem volume were converted to biomass by BEFs (I) while the biomass estimate of coarse roots and stump for broadleaved sites was based on study by Laitakari (1935). The foliage biomass of broadleaved forests was assumed to be proportional to branch biomass, and this proportion decreased from 80% to 20 % with an increasing stand age. The fine root biomass of stands was assumed to be proportional to foliage biomass, based on the functional balance theory (Davidson 1969) and discussed by Mäkelä (1990). The parameter values for these proportions were based on various studies (Helmisaari and Hallbäcken 1998, Vanninen and Mäkelä 1999, Cronan 2003). The biomass of the understorey vegetation was estimated with models developed by Muukkonen et al. (2005) with parameter values reported in Peltoniemi et al. (2004).

Thereafter, the litterfall of each biomass component was estimated using componentspecific biomass turnover rates (Table 4). Those rates for branches were reported elsewhere (IV, V), while the turnover of foliage was based on other studies (V)(Muukkonen 2005). The turnover rates of bark and cones were based on various studies (Viro 1955, Mälkönen 1974, 1977), while fine root turnover was estimated based on findings by Kurz et al. (1996) and Majdi (2001). The turnover of understorey vegetation was based on several studies (Mork 1946, Tamm 1953, Head 1970, Mälkönen 1974, Kellomäki et al. 1977, Havas and Kubin 1983, Longton 1992, Nakatsubo et al. 1997, Kumpula et al. 2000).

The amount of litterfall was based on the biomass of each component (foliage, branches, stem, coarse roots and fine roots) and their turnover rates (Table 4). The soil carbon stock and changes occurring in it were estimated with the Yasso soil carbon model (Liski et al. 2005). The Yasso model has seven pools (Fig. 1) and it simulates the changes and stocks of carbon based on litterfall, its quality, temperature sum (zero degree threshold) and drought index (rainfall – potential evapotranspiration).

Litter formed the input to the soil model and it was grouped to non-woody, fine woody and coarse woody litter. Two out of these seven pools in the model were for litter and rest five were for decomposition. Five decompositions pools were named according to their content and function, these pools are extractives, celluloses, lignin-like compounds, humus 1 and humus 2 (Fig. 1). Non-woody litter formed directly extractives, celluloses and lignin-like compounds that were located to decompositions pools. Woody litter was defined according to its size and origin whether it was fine or coarse woody litter. Both these litter types had Table 4. Turnover rates for biomass components by species and location (southern and northern Finland), indicating the ratio of biomass that is shed annually.

	Trees						
	Spruce forests		Pine forests		Broadleaved		
					fores	ts	
	Sª	N⁵	S	Ν	S	Ν	
Foliage	0.10 [℃]	0.05°	0.21 ^d	0.10 ^d	0.	78 ^e	
Branches & roots	0.0)125°	f(t) ^f		0.0135 ⁹		
Stump bark	0.0) ^h	0.0030		0.0001 ^j		
Reproductive origins & stem bark	0.0027 ^h		0.0052 ⁱ		0.0029 ^j		
Fine roots	0.811 ^k		0.868 ⁱ		1.	0 ^m	
	Understorey vegetation						
Bryophytes	0.33"						
Lichens	0.1°						
Dwarf shrubs, aboveground	0.25 ^p						
Herbs & grasses, aboveground	1 9						
Dwarf shrubs, belowground			0.33 ^r				
Herbs & grasses, belowground	0.33ª		.33 ^p				

^a Southern Finland

^b Northern Finland

^c (V)

^d (Muukkonen 2005)

e Leaves of broadleaved trees became 22% lighter during yellowing process in autumn (Viro 1955)

^f As a function of age, based on (IV)

^g Estimated from the repeatedly measured permanent sample plots of the Finnish National Forest Inventory

^h Derived from the results of Viro (1955)

ⁱ Derived from the results of Viro (1955) and Mälkönen (1974)

^j Derived from the results of Viro (1955) and Mälkönen (1977)

^k (Majdi 2001)

¹ (Kurz et al. 1996)

^m We assumed that broadleaved trees replace all their fine roots each year

ⁿ Rough estimation that the litterfall equals the annual biomass production (Tamm 1953, Kellomäki et al. 1977, Havas and Kubin 1983, Nakatsubo et al. 1997)

° Rough estimation that the litterfall equals the annual biomass production (Longton 1992, Kumpula et al. 2000)

^p Rough estimation that the litterfall equals the annual biomass production (Mork 1946, Mälkönen 1974, Havas and Kubin 1983)

^q Aboveground parts of herbs and grasses change completely into litter at the end of the growing season

^r Rough estimation that the life expectancy for roots is about 2–3 years (Head 1970)



Figure 1. Flow chart of soil carbon model Yasso, boxes represent carbon pools, while arrows indicate carbon fluxes. According to Liski et al. (2005).

rates that define the translocation of matter to decomposition pools. All five decomposition pools have decomposition rates defining annual mass loss, these decomposition rates depend on effective temperature sum with 0 °C degree threshold and summer drought index (Liski et al. 2005). The effect of effective temperature sum was included when soil carbon stocks and their change were estimated, while drought index was ignored (VI).

Within the model the slowest decomposition pool was the humus 2 pool where carbon locates several hundreds or even thousands years. The fastest pools were those for extractives, celluloses and lignin-like compounds dominating the rapid changes in soil carbon since short residence time. The results of Liski et al. (2005) indicated that Yasso soil model estimated well soil carbon stock changes, while the estimates for soil carbon stock deviated from the measurements by 15%. According to Liski et al. (2005) the soil carbon stock change by Yasso was most sensitive to humification fractions and decomposition rates of humus. It was also found that the decomposition parameter of humus was most uncertain. They also found that 1% change in the effective temperature sum (equal to change of 0.1 °C of mean annual temperature) influenced soil carbon stock change estimate by 0.49 or 0.71%, while similar change in drought index changed it by 0.1% only (Liski et al. 2005).

The carbon pools of biomass, litter and soil were estimated separately for southern and northern Finland (VI), and the input variables of soil carbon model were estimated for these regions. Changes in land use impacted to soil modelling and were taken into account by assuming that the land area either added or removed from forest land had a carbon stock that equalled the mean carbon stock of the first year of simulation (6.1 kg C m⁻²). This was done because either the previous or the subsequent land-use or its carbon density was not known throughout the study period.

Covering all the pools and major fluxes of forests since the 1920s with the NFI data and soil carbon model allowed the evaluation of forest development through the use of ecological concepts (VI). These concepts include NPP (net primary production) (Eq. 5), which was here the sum of carbon stock C change of trees and understorey, litter production L of trees and understorey, natural losses M and fellings F.

$$NPP = \Delta C + L + M + F \tag{5}$$

Thereafter, we derived the NEP (net ecosystem production) (Eq. 6), which equals the NPP minus the heterotrophic respiration from the soil model (Liski et al. 2005).

$$NEP = NPP - R_h \tag{6}$$

The NBP (net biome production) (Eq. 7) was estimated by deducting removals RE from the NEP, which contains roundwood removed from the ecosystem.

$$NBP = NEP - RE \tag{7}$$

Here NPP, NEP and NBP take into account major fluxes of intensively managed forests of Finland, but noting that our estimate for NEP excludes all non-CO₂ fluxes, e.g. carbon monoxide, methane, dissolved inorganic and organic carbon (Randerson et al. 2002). Our estimate of NBP is based on the NEP minus removals and other disturbances like storms and fires are taken into account already by NPP, meaning that growing stock is decreased by these events, which further has impact to carbon stock changes. It has to be noted that removals are

the main disturbances currently within Finnish forests, while forests are successfully protected against uncontrolled fires, and annual area burned being less than 1200 ha since 1973 (Metla 2004). In addition to removals and fires also abiotic damages (wind, snow, etc.) have reduced the quality of stands within 6.1% of forest lands according to latest NFI (Metla 2004). It has to be noted that our estimates of these ecological equivalences imply only on mineral soils due to fact that organic soils and estimation of their gas exchange are excluded (VI).

RESULTS

Biomass estimation

The results showed that BEFs, can be established by using representative biomass equations and tree-level data and that they are applicable within the region of the source data (I, II). The BEFs modelled for total biomass of Scots pine were stable as a function of stand age, while the BEFs for Norway spruce decreased as a function of stand age (I). The RSEs of the total BEFs including sampling and model errors were estimated by age-classes (I). The RSE varied between 3% and 20%, depending on species and age-class (Fig. 2).

The BEFs for biomass components (e.g. foliage, branches and roots) were dependent on stand age. The BEF for foliage decreased (Fig. 3), while the BEFs for stems increased as a function of stand age. The BEFs for coarse roots and stump were relatively stable as a function of stand age (Fig. 3).



Figure 2. Biomass expansion factors (Mg m⁻³) for Norway spruce and Scots pine stands according to ageclasses. Errors bars denote 95% confidence intervals.



Figure 3. Biomass expansion factors (Mg m⁻³) for different biomass components (foliage, branches, stem and coarse roots plus stump) of Scots pine, Norway spruce and broadleaved stands as a function of stand age.

Testing biomass estimation

Biomass estimation for Sweden

Biomass estimation with BEFs (I) was tested against tree-level biomass estimation (II). The biomass estimate for Sweden (excluding mixed stands) with age-dependent BEFs (I) was 6.7% lower than the estimate obtained with the tree-level NFI data and equations by Marklund (1988). The RSE estimates were slightly higher for estimates based on age-dependent BEFs than for those based on the tree-level approach. The RSEs of both approaches varied between 10% and 20% (Fig. 4).

For the northern parts of Sweden such as Norra Norrland, BEFs resulted in lower biomass estimates for Norway spruce sites compared with tree-level biomass estimation, while in southern regions such as Götaland BEFs resulted in overestimation of biomass (Fig. 4).

For Scots pine sites, the biomass estimates obtained with different methods agreed rather well in southern and northern Sweden (Fig. 5). The BEFs (I) gave slightly lower estimates for biomass than the tree-level equations of Marklund (1988). The RSEs were slightly larger for estimates obtained with BEFs (Fig. 4).



Figure 4. Aboveground biomass estimates with relative standard errors (RSEs) for Norway spruce sites in Norra Norrland and Götaland in Sweden obtained with tree-level NFI data and Marklund's (1988) equations compared with an estimate obtained with aggregated NFI data and BEFs (I).



Figure 5. Aboveground biomass estimates with relative standard errors (RSEs) for Scots pine sites in Norra Norrland and Götaland in Sweden obtained with tree-level NFI data and by Marklund (1988), compared with an estimate obtained with aggregated NFI data and BEFs (I).

Estimation of foliage biomass

Both the preciseness and accuracy of foliage biomass estimates were dependent on the detail of measurements available (III). The foliage biomass estimates obtained with BEFs were in general unbiased when compared against an independent dataset for Scots pine stands, having a slope close to 1 between the modelled and predicted biomasses (Fig. 6). However, the foliage biomass values for Norway spruce stands were overestimated when BEFs were used, especially with fully stocked stands, the slope being 1.195 (Fig. 6).

The foliage biomass estimated as a function of stem volume were systematically underestimated for southern Finland with Scots pine stands, but agreed well with Norway spruce stands (Fig. 6). The variance of the slope parameter was high, especially for Scots pine stands, which emphasizes the difficulty in foliage biomass prediction of a single stand with scarce information.

The predictors used (stem volume and stand age) were not sufficient to estimate the foliage biomass of a single stand (I). On the other hand, data on individual tree dimensions (dbh, height and crown base height) and biomass equations parameterized in Sweden



Figure 6. Modelled foliage biomass vs. predicted foliage biomass for Scots pine and Norway spruce, based on BEFs and volume to biomass model (I) and an approach presented by Valentine et al. (1994) as applied in (III). The regression was fitted through the origin and slope and its standard error is indicated below the panels.

(Marklund 1988) and with fellings in Finland (Hakkila 1991) resulted also in biased biomass estimates, with slopes varying between 0.59 and 1.21 for modelled and predicted foliage biomass (Fig. 7).

When the quantity of information used increased, and either Valentine's approach or biomass equations parameterized with reference data were used, both the preciseness and accuracy of estimates improved (Figs. 6 and 7).

The biomass models of Hakkila (1991) and Marklund (1988) gave systematically different estimates for foliage biomass (Fig. 7), while the biomass model parameterized with reference data agreed well with the predicted biomass.

Estimating biomass flows with turnover rates

The combination of the biomass distribution model of crown and crown base height measurements from 1985–1986 and 1995 made it possible to obtain estimates for the annual potential branch litterfall, which were an average of 2.7% and 1.25% as a proportion of branch biomass for Scots pine and Norway spruce, respectively (IV, V). Potential branch litterfall was dependent on the tree size (dbh) and stocking density. In dense stands the crown base



Figure 7. Modelled foliage biomass vs. predicted foliage biomass for Scots pine and Norway spruce, based on biomass equations (Marklund 1988, Hakkila 1991) and (III). Regression was fitted through the origin and slope and its standard error is indicated below the fit.

of trees increased in height more quickly and trees produced more branch litterfall, relative to their branch biomass. According to the estimated models the relative branch litterfall in Norway spruce stands varied between 3% and 0.5% and in Scots pine stands from 7% to 1%, depending on stand density.

For Scots pine sites with measured litterfall, the modelled branch litterfall based on tree size and stocking density did not correlate (Fig. 8), but estimates were within the range of measurements (IV). On the other hand, the litterfall estimates obtained with average turnover rates were systematically overestimated for the Scots pine sites (Fig. 8). For Norway spruce stands the litterfall estimation obtained with models (V) produced systematically lower estimates, especially for southern Finland (Fig. 8). Estimates obtained by average turnover rate for Norway spruce were closer to the measured litterfall. With Scots pine sites predictions improved when more information was used and bias was reduced, while with Norway spruce additional information (dbh and stocking) increased the bias.

These models are suitable for estimating regional branch litterfall and carbon flows of branch litter if more sophisticated estimation methods for branch litter do not exist. Applying these models for estimating branch litterfall of an individual stand may lead to biased results, especially if conditions at each individual site deviate strongly from the average (Fig. 8).



Figure 8. Branch litterfall (kg ha⁻¹) for Scots pine and Norway spruce, measurements vs. models, in which black symbols represent modelled litter with average turnover (2.7% Scots pine and 1.25% Norway spruce as a proportion from branch biomass), while open markers represent results of branch litterfall estimated with tree-level models, in which turnover is based on tree size and stocking (IV, V).

Measurements showed that Norway spruces in southern Finland shed needles with 50% probability when the age of the needle cohort was 5.5 years and that they shed needles simultaneously with several needle cohorts (V). Combination of measured needle shed dynamics and the yellowing effect reported by Viro (1955) revealed that the turnover rate for needles of Norway spruce in southern Finland was 0.1, while based on data reported by Flower-Ellis and Mao-Sheng (1987) turnover rate for foliage was estimated to be 0.05 for northern Finland.

Integrated method for estimating forest carbon budget

Forest inventory data, biomass models, biomass turnover rates and the soil decomposition model were combined to derive estimates of tree and soil carbon pools and the changes occurring in them. The tree carbon stock in Finland (VI) increased from 510 Tg to 780 Tg from 1922 to 2004 (Fig. 9). The increase was partly due to increase in forest area, but also due



Figure 9. Development of carbon pool of biomass (A) and carbon flux as litter (B) produced by living trees according to biomass components, in Tg of carbon.



Figure 10. Distribution of carbon in trees by stand age-classes in southern and northern Finland, in Tg of carbon.

to intensified silviculture and due increased difference between increment and drain (Metla 2004 p. 43) that has increased the average stocking per area unit, especially after the 1960s.

The annual litterfall from living trees (foliage, branches, cones, bark, coarse roots and fine roots), harvesting residues, understorey litter and tree mortality increased from 18 Tg to 25 Tg of carbon (Fig. 9) during the period investigated (VI). This increase resulted from increases in growing stock and in the forested area. Most of the tree biomass is located in stems, roots and branches, while the major part of the litter input to soils is composed of short-lived biomass components such as fine roots and foliage (Fig. 9). Using age-dependent BEFs (I) made it possible to estimate biomass of forests in Finland during the 82 year period, with changing age-class distribution (Fig. 10), and moreover that facilitated the estimation of litterfall more accurately through the study period.

The relative biomass pool and litterfall from living trees varied slightly during the 82 year period, due to changes in the age-class distribution, which affected the relative biomass distribution by component (foliage, roots etc.), which further changed the relative litterfall (Fig. 11). The effect of altered age-class distribution on relative litterfall can be seen in northern Finland, where foliage and fine roots made up 80% of the total tree litter during the 1920s. Thereafter, changes in younger age-classes (Fig. 10) increased the relative share of foliage and fine roots to 82% of the total litterfall (Fig. 11).



Figure 11. Relative biomass pool (A) and litterfall (B) in the 1920s and 1990s in northern and southern Finland (VI).



Figure 12. Tree and soil carbon stocks (A) and changes occurring in them (B) between 1922 and 2004 in Tg of carbon (tree stock from all soils, while soil stock comprised mineral soils).

The difference between the relative proportion of foliage litterfall in northern and southern Finland was notable. This difference was due to changes in needle longevity across the geographic gradient of Finland. Needle litter turnover was estimated to be in northern Finland half (Table 4) the level in southern Finland (V) and (Muukkonen 2005).

Both the tree and soil carbon stocks showed long-term increasing trends (VI). The carbon stock of trees increased by 270 Tg during the 82 year study period, while the soil carbon stock increased from 847 Tg to 959 Tg (Fig. 12). Both the carbon pools of trees and soil varied annually due to commercial harvests and climate (Figs. 12 and 13). Both the trees and soil changed from sink to source and vice versa with no dependence on each other, especially before the 1970s. Since then both pools have acted as sinks, except for a few years when soil was likely a source. Carbon stock changes of trees in Finland have varied from -5 to 15 Tg annually, while soils varied from a source of -6 Tg to a sink of 8 Tg of carbon. In addition, the annual carbon exchange throughout the Finnish forests ecosystem (including trees, understorey and soils) has varied from -9 to 20 Tg.

Heavy loggings in 1950 reduced the tree carbon stock temporarily, which increased the quantity of harvest residues, but decreased the litterfall of living trees, which can be seen as a reduction in total litter input during the 1970s (Fig. 13) and eventually as a small decrease in the soil sink (Fig. 12).



Figure 13. Soil carbon stock, total litter input (A) per area (g C m⁻²) and temperature sum (B) of southern Finland (with 0 °C threshold) between 1922 and 2004 (VI).

We estimated the change in soil carbon stock in mineral soils based on estimated litterfall, climatic data and the dynamic soil carbon model (VI). We found that most of the increase of soil carbon stock was due to increase in the forest area, while the mean carbon density of soil increased from 6.10 kg m⁻² to 6.34 kg m⁻² between 1922 and 2004 and fluctuated heavily (Fig. 13). Our modelling scheme suggests that changes in the soil carbon stocks were influenced by temperature and litter input to the soil (including living trees, understorey, natural mortality and harvesting residues of stems, stumps, canopy and roots) (Fig. 13).

Soil carbon model Yasso is temperature driven, and due to that soil carbon stock reacts immediately for annual fluctuations within effective temperature sum (Fig. 13). Moreover, the total litterfall per forest area has increased steadily since the 1970s, which was partly due to increase in the amount of litter by increased forest vegetation and due to increase in harvestings, resulting more harvesting residual. According to study (VI) soil carbon density has been rather constant since 1960's, but an increase can be detected during 1990's, which results from increasing trend in litterfall since 1975 (Fig. 13). It seems that soil carbon stock is adjusting with a lag to a new level resulting from increased litter.

The soil carbon stock was influenced by previous land use. During our modelling of soil carbon we assumed that the soil carbon density of the transferred land equalled the initial carbon density of forested land in 1922. During the 1990s, two thirds of the carbon accumulation in soils was due to increase in forested areas, due to fact that forested areas increased by 1.5% according to our calculation scheme for mineral soils in the 1990s (Fig. 14).

We found that the major fluxes in Finland's forests were biomass production and decomposition, in which decomposition accounted for more than 70% of biomass production, while removals accounted for 15% in the 1990s (Fig. 14). The major input to the forest biome was biomass production, while a minor input consisted of soil carbon originating from other land uses that were transformed to forest, but noting that soil carbon from previous land-use were allocated to the pools of Yasso that decompose slowly and therefore have long lasting effect to soil carbon stock.

Deriving ecological variables from our calculation and modelling scheme gives insight to the development of Finland's forests. The NBP has been positive since the 1970s (Fig. 15) and negative in the 1930s and 1960, partly due to intensive loggings (VI). During this 82 years study period, the average annual NPP has increased from 0.3 to 0.4 kg m⁻² (Fig. 15).



Figure 14. Stocks and fluxes of carbon during the 1990s in kg C $m^{-2} y^{-1}$.



Figure 15. Development of Finland's forests according to NPP, heterotrophic respiration, NEP, removals and NBP in kg C m⁻² y⁻¹.

DISCUSSION

Biomass estimation

Biomass estimation for national inventory reports of GHG in most European countries has relied on simple conversion factors that convert stem volumes to biomass (Tomppo 2000, IPCC 2003). These robust conversion factors often lack uncertainty estimates and may be based on only a few sites with intensive measurements (Löwe et al. 2000).

Here we developed BEFs that were based on the biomass equations of Marklund (1988), which cover extensive biomass data from Sweden and have been estimated to be best available biomass equations for Finnish conditions (Kärkkäinen 2005). The different origin of sampled biomass and sampled stem volume might lead to biased BEFs, as tested in the study I Swedish stem volume equations (Brandel 1990) gave equal results when compared to Finnish volume models (Laasasenaho 1982) that were applied here. Both biomass and volume equations were applied to permanent sample plot data from Finland's NFI. Assuming that the biomass allometry of trees in Finland is similar to that of Sweden, these BEFs can be used for regional biomass estimation in Finland. This assumption of similarity of biomass allometry was tested within (III), where foliage biomass estimates by Marklund (1988) were plotted against independent predictions based on measurements from southern Finland. According to (III) it was found that foliage biomass estimates were biased $\pm 20\%$ for southern Finland depending on species, while noting that foliage biomass is the most difficult and minor aboveground biomass pool of trees to be estimated.

Previous conversion factors applied in Finland by Tomppo (2000) were published by Karjalainen and Kellomäki (1996). These values of conversion factors were lower for conifers than BEFs developed in the study I, when we compared the values by assuming the wood densities reported by Karjalainen and Kellomäki (1996). For Scots pine, the mean conversion factor was 0.71 (I), while the factor reported by Karjalainen and Kellomäki (1996) was 0.6. For Norway spruce the conversion factors were 0.81 and 0.72, according to (I) and (Karjalainen and Kellomäki 1996), respectively. For broadleaved stands Karjalainen and Kellomäki (1996) reported a value of 0.82, while we obtained an estimate of 0.74 (I) as a mean (by assuming that the roots and stump constituted half the stem (Laitakari 1935), excluding the leaves). In comparison to the BEFs from the UK obtained by Levy et al. (2004),

the values for Scots pine agree well, being 0.71, if the density is assumed to be 0.39 Mg m⁻³. For Norway spruce the total BEF was 0.74 based on Levy et al. (2004), assuming a wood density of 0.385 Mg m⁻³, which agrees well with our estimated total BEF (I).

The relationship of BEF with total biomass and stand age correlated negatively with Norway spruce (I). Similar patterns of relative increase in stem biomass have been found for BEFs with tree height (Levy et al. 2004) and with increasing stem volume in China (Fang et al. 1998).

We estimated the degree of uncertainty of the BEFs in terms of RSE (I). These errors were relatively large, especially in young age-classes with limited numbers of observations such as young (10–30 years) Norway spruce sites.

The aim of the study I was to facilitate regional and national biomass estimation in Finland; the BEFs were developed with biomass equations based on extensive sampling (Marklund 1988) and on large numbers of NFI plots. The biomass models provide estimates that are averaged, and the BEFs models are also averaged over wide range of variation. Thus, biomass estimation with BEFs developed in this study provides average estimates of biomass that do not take into account site-specific conditions that affect biomass allocation (such as fertility and climate).

Applicability of BEFs in biomass inventory

The regional biomass estimates obtained with BEFs (I) agreed moderately with the tree-level biomass estimates for Sweden (II). The estimates agreed well, especially in central Sweden for Norway spruce, while the largest relative disagreements were found with Norway spruce stands in southern Sweden (Svealand and Götaland regions). The biomass of broadleaved sites were also overestimated for the northern regions.

In conclusion (II), BEFs should be locally developed and an application of local biomass and stem volume data would be advisable when these factors are formulated. Anyhow, if one is applying biomass equations from neighbouring regions either directly with tree level data or in order to formulate BEFs, the applicability of these equations should be evaluated against independent data sets in order to quantify possible bias. Typically biomass studies reflect the allometry resulting from the history of growing conditions and management. If independent biomass data sets for testing don't exist it would important to study the sample of applied biomass equations, weather it reflects the sample that it is going to be applied with (Kärkkäinen 2005).

The BEFs were developed, based on plots that had stem volumes less than 250 m³ ha⁻¹ (I). Thus the biomass estimates with age-dependent BEFs were biased in Götaland, where the mean stem volumes were up to 350 m³ in mature Norway spruce stands, while the stem volumes were up to 250 m³ in (I) when BEFs were developed.

Limitation of BEFs with high stem volumes relates to the biomass proportions of trees that stabilise after canopy closure (Oliver and Larson 1996 p. 79). In several ecophysiological models the biomass of foliage was predicted to stabilize or even to decrease after canopy closure (Bassow et al. 1990, Berninger and Nikinmaa 1997, Mäkelä 1997). In comparison, empirical biomass equations predict that foliage biomass increases as a function of dbh, which can be seen from the equation compilations by Zianis et al. (2005) and by Ter-Mikaelian and Korzukhin (1997). This increase in foliage biomass as a function of diameter may hold at tree-level, but is misleading at the stand-level with closed canopy and constant stocking density, when a tree increase for diameter but no longer in foliage biomass.

Empirical models of biomass, e.g. biomass equations and BEFs, normally do not take into account the effect of competition on biomass allocation. Biomass measurements, biomass equations and BEFs of a specific time point reflect the competition status and biomass allocation that occurs during the sampling. Thus, most empirical biomass models are likely to have difficulties to predict biomass when silviculture changes, e.g. changes in stand density regimes affect the biomass proportions and especially the biomass allocated to canopy (Vanninen and Mäkelä 2000, Ilomäki et al. 2003).

Error estimates for biomass estimates with BEFs and the Swedish NFI data were slightly higher than those based on tree wise data and Marklund's equations (1988) (II). The error estimates for BEFs were based on the concept presented in the study and included both sampling and model error, although the uncertainty of parameter estimates of the biomass and volume equations were not used in the error estimates for these BEFs and the uncertainty of stand age estimate was excluded. The error estimates for the aboveground biomass stock of Sweden either with BEFs or equations were rather small, with RSEs varying from 10% to 20% according to tree species, regions and age-classes. The difference between tree-level and BEF-based biomass estimate (6.7%) emphasizes the danger of systematic error in biomass models (e.g. BEFs).

Estimating foliage biomass

Our ultimate aim was to estimate the changes occurring in soil carbon stock based on an inventory approach (Kurz and Apps 1999, Liski et al. 2002) in (VI). Within this approach foliage biomass estimation plays a key role (VI). In this approach, both litterfall from foliage and litter produced by fine root senescence were dependent on foliage biomass, which was estimated with BEFs (I). The fine root biomass was estimated with a species-specific ratio to foliage biomass because appropriate biomass equations or conversion factors for fine root biomass did not exist.

The foliage biomass is the most challenging aboveground biomass pool to be estimated due to its functional tasks and rapid turnover compared with woody components that accumulate during tree growth (Zhang et al. 2004). Various methods for estimating foliage biomass were tested against plot-level biomass predictions that were up-scaled from branch-level measurements (III). For the Scots pine stands measured, the BEFs produced regionally unbiased results for foliage biomass, but with relatively high variance (Fig. 6). In comparison, the BEFs with Norway spruce stands overestimated foliage biomass at sites that had high stem volume values and underestimated it with low values of stem volume. The variance was lower compared with the BEFs for Scots pine (Fig. 6).

The systematic error of foliage biomass estimates obtained with the BEFs for Norway spruce may have been partially due to the fact that the sample of biomass data used was located in southern Finland (III). The sampling procedure by Marklund (1987) also differed from the sampling of the reference data described (III). In addition, the reference material described originated from southern Finland and included stands from coastal areas, while the data of Marklund (1988) originated from the whole of Sweden, but mainly from inland regions where 90% of the sites are more than 100 m above sea level (III).

The biomass equations of Hakkila (1991) and Marklund (1988) both underestimated foliage biomass of Scots pine stands, which may indicate that the sample of trees may have included more fertile sites having more foliage than did the sample of both biomass studies compared (III). For Norway spruce plots Hakkila (1991) slightly underestimated foliage biomass, while Marklund (1988) overestimated it.

Most unbiased estimates and low variances were found when foliage biomass estimation was performed either with tailor-made biomass equations or with a method described by Valentine et al. (1994). The information needed for biomass equations was tree-level dbh and height, while Valentine et al. (1994) approach was applied with stand-level basal area, crown ratio and pipe model ratio. Both methods appeared to be applicable to an estimation of foliage biomass in a single stand, although it must be remembered that these methods were parameterized with the reference data.

To estimate forest biomass regionally and at the stand-level, the combination of empirical data collected with NFI methods and assumptions concerning biological relationships from ecophysiological models could be used. For example, the combination of basal area, crown height and various pipe model ratios (Shinozaki et al. 1964, Mäkelä 1990) for foliage, branches and roots, as proposed by Valentine et al. (1994) and tested here for foliage (III), could be used in national biomass estimation (e.g. for GHG inventories).

The attractiveness of the combination of NFI measurements with pipe model ratios is that in addition to basic variables such as basal area and crown height, only models for pipe model ratios would be needed. Thereafter, estimating the biomass of canopy and roots in addition to stem biomass (which is already estimated due to its commercial value), would be a rather simple task to do. Here (VI) we applied the BEFs (I) to estimate biomass, since the inventory variables available from the 1920s to 2000 were aggregated stem volumes. However, more sophisticated biomass estimation methods such as presented here (III) modified from Valentine et al. (1994), could be used with the tree-level data of the latest inventories.

Litterfall estimation

Most of the litterfall measured with litter traps has been focused on foliage and reproductive organs (Liu et al. 2003), and the measurements of litter from large branches are very limited. In the present study, updated litterfall estimates for branches were made available, based on various models and measurements. Previously applied values, e.g. by Liski (2002), were means for whole boreal zone derived from the biomass data compilation by de Angelis (1981).

In our modelling scheme, more precise litterfall estimates for branches and foliage also improved soil carbon change estimates for Finland (VI). The major goal was to estimate the turnover rates for branch biomass and also for that of foliage biomass of Norway spruce (IV, V). Combination of models for biomass distribution and crown rise made this possible, and we obtained estimates that can be used with regional litterfall estimation.

The branch litterfall estimates of Scots pine stands were improved, when the model with dbh and stocking was applied, while using a constant turnover overestimated litterfall (Fig. 8). Branch litterfall estimation was more challenging for Norway spruce, in which a non-linear model with dbh and stocking explained only 62% of the variance of potential branch litterfall, while for Scots pine this figure was 85%. Comparison with measurements of branch litterfall of Norway spruce sites also indicated that modelling with dbh and stocking underestimated litterfall, while the constant turnover rate was more accurate. On the other hand, the estimated needle litterfall for Norway spruce agreed well with measurements from several litter trap studies (V). This difficulty in branch litterfall estimation may be due to the stochastic nature of the timing of branch fall, which is dependent on branch death, and after that depending on surrounding trees, winds and decomposition rate of branch. These sites with measured litterfall are rather old, and partial underestimation at Norway spruce sites may have been due

to growth patterns, in which the branches remain attached to the stem long after they have died. In addition, modelling of branch litterfall ignored the branch litterfall from the inner canopy, which may be substantial, especially for Norway spruce trees (IV, V).

Integrated method for estimating forest carbon budget, application to Finland

Using the forest inventory-based approach to quantify all 5 carbon pools listed by the IPCC (2003) was found feasible. The sample plot data gathered by the NFI covered all conditions across the geographical gradient. We focused our application on mineral soils because the Yasso soil model was not applicable to peatlands (Liski et al. 2005). By ignoring peatlands we excluded a 4600 Tg carbon pool in Finland (Kauppi et al. 1997). In general, the carbon pools of forests and soils increased during the period of investigation, partly due to land-use change and partly to the increasing biomass density that increased litter production and eventually the soil carbon stock.

The most interesting temporal pattern in our calculation and modelling scheme was inclusions of the variability caused by commercial loggings and variation in interannual growth. These phenomena had an impact on tree and soil carbon stocks, which varied strongly on a yearly basis, from source to sink and vice versa. We also found that heavy loggings decreased the biomass pool temporarily, while increasing that of soil in the short term. On the other hand, warm periods decreased the soil pool by stimulating decomposition, while the biomass pool increased due to favourable growing conditions. The soil carbon pool reacted immediately to increasing temperatures through enhanced decomposition (Fig. 13). Similar results were reported, based on measurements by Braswell et al. (1997) who found a correlation between temperature and CO₂ growth rate with zero lag, indicating rapid reaction of the microbial community to increase in temperature. They also found a positive correlation with vegetation index and temperature, with a lag of 1-2 years, indicating slower response of the vegetation to increased temperature. Similar pattern can be seen from our calculation and modelling scheme, in which we assume that the most of the decomposition is driven by temperature and where annual tree growth results from growth indexes based on NFI measurements.

In our calculation scheme (VI), the biomass carbon pool increased by an average of 27 g C m⁻² annually in the 1990s (Fig. 14), while the carbon pool of soils increased by 11 g C m⁻², including the effect of land-use change, which was close to nil during 1990's . This effect was taken into account by increasing the assumed carbon density of soil that was converted to forest. A study by Hurtt et al. (2002) reported similar values for the biomass carbon sink of the coterminous United States, which was 40 g C m⁻² annually in the 1980s, while their estimate for soil and litter pool change was 52 g C m⁻² annually. These changes in the carbon pools of the USA were mainly driven by changes in land use and suppression of fires. Both Hurtt et al. (2002) and Houghton et al. (1999) showed that US forests were a source of carbon during the 1800s due to extensive wild fires.

We showed that ecological equivalences, such as NPP, NEP and NBP can also be derived from forest inventory data if the proper biomass, litter and soil decomposition estimation methods are available (VI). Noting that peatlands and non CO_2 fluxes were excluded from our definition of above mentioned ecological equivalences. Based on models and inventory data (VI), our estimate for the average NPP for Finland during the 1990s was 374 g C m⁻² annually (Fig. 14). In comparison, Gower et al. (2001) reported average NPPs of from 214 to 351 g C m⁻² annually for sites in Ilomantsi, eastern Finland, while Pregitzer and Euskirchen (2004) reported an average NPP for boreal region of 280 g C m⁻². For the mean NEP of Finland in the 1990s, we obtained 110 g C m⁻² annually (Fig. 15), which was within the range of measurements by Kolari et al. (2004), in which the NEP varied between -262 and 252 g C m⁻² annually, depending on site age but always more than 200 g C m⁻² annually in stands 40 years of age. These comparisons with other approaches reveal that estimates are same order of magnitude, but not much more. Forest inventory based approach to estimate carbon fluxes and ecological equivalences was based on main carbon fluxes of Finnish forests only and the up-scaling from NFI data introduced uncertainties that are often difficult to quantify.

The most challenging carbon pool to quantify was the soil pool, especially the changes occurring in it. We ran the soil model with estimated litter input and climatic data (VI) and noted that our soils vary heavily from sink to source, mainly depending on loggings and temperature. We also observed that the biomass and soil pools react differently for changing conditions such as harvestings and temperature increase.

Upland forest soils have acted as a sinks of 11 g C m⁻² annually in the 1990s, or 10.7 g C m⁻² annually if the effect of increased forest area was excluded (Fig. 14); this increase of 11 g C m⁻² annually probably resulted from increased litter production by trees. A study by Akselsson et al. (2005) reported an average annual increase of 18 g C m⁻² for soil organic matter in mature forests from Sweden. They used the concept of limit values, estimating the litter remains based only on foliage litterfall. In Finland, Peltoniemi et al. (2004) detected an average change of 4.7 g C m⁻² annually for the organic layer, based on a sample of forest stands of varying age. They also compared stand-level estimates, based on simulations with the Yasso soil model (Liski et al. 2005) against measurements using concepts similar to those used here (VI), and found that the simulations agreed rather well with the measurements, observing a modelled change of 5.8 g C m⁻² annually for the organic layer. Wardle et al. (2003) estimated that during 100 years without forest fire additional 0.49 kg m⁻² were stored to humus layer of forested islands in Sweden, which agrees well with measurement and simulations of Peltoniemi et al. (2004). Still, the measurements and modelling of the carbon stock changes in soils are associated with high levels of uncertainty (Ståhl et al. 2004, Liski et al. 2005, Monni et al. 2005).

During our modelling and calculation exercise (VI) we used biomass estimation methods (I) combined with litterfall rates derived elsewhere (IV, V) and from various publications (Table 4). The biomass estimates and their turnover formed the litter input to the soil model. Soil model parameterization is under constant development, and these relatively high levels of uncertainty are decreasing. In addition, the litter input was also associated with relatively high degrees of uncertainty, especially those of foliage and fine roots. These short-lived biomass components form 80-90% of litterfall (Fig. 11). Here the biomass estimation was mainly based on the use of BEFs (I), but BEFs and biomass equations do not exist for fine roots and thereafter we assumed that fine root biomass was proportional to foliage biomass, based on the assumptions of the functional balance theory. However, our estimates for the fine root biomass to foliage biomass ratios were probably underestimated for northern Finland, because the ratios currently are based on studies undertaken in southern Finland with more fertile soils. On the other hand, the fine root turnover rates are likely overestimated for northern Finland for the same reason, since these rates are based on sites with higher fertility and favourable temperatures compared with those in northern Finland (Majdi 2001). Further information is needed on fine root biomass and its turnover rate across the climatic gradient of Finland. This knowledge is also needed to test the longer life span estimates for fine roots obtained with isotope tracer applications (Gaudinski et al. 2001, Matamala et al. 2003).

Carrying out the calculation scheme (VI) revealed the importance of land-use change estimation, especially the value of detailed land-use change matrices. The forested area of Finland has increased since the 1950s, but the previous land use is not always known. Furthermore, the previous carbon stocks of biomass and soil are also unknown, as are the time spans of the carbon pool adjustment after the land-use changes. For example, if a country converts large areas of fully stocked forests to agriculture and meanwhile converts bare land to forests, the net change in the forested area may be nil, but actually a large biomass pool is lost. Combination of the methods and models used (VI) with a historical land-use change matrix, as Hurtt et al. (2002) did for the USA, would be an interesting way to proceed with modelling of the carbon stock change scenario for Finland.

These results underline the importance of complete accounting when carbon pools and the changes that occur in them are examined. In other words, the tree pool as a sink does not imply that the soil pool is also a sink. Moreover, completeness is also needed for land-use change detection, including knowledge of the stocks of previous and following land uses and time of the adjustment of stocks under new land use. Complete counting is also needed if forest management is used as a tool to mitigate climate change, since some management options that will enhance tree biomass production may decrease other existing carbon pools such as soils or dead wood and vice versa.

The methods presented here and combined in (VI) to estimate carbon budgets for Finland include various assumptions and include vast amount of sources of uncertainties. First question that rises is that whether our calculation scheme (VI) is build in realistic way, when we are relying on the assumption on biomass allometry, litterfall and decomposition. Here only small parts of these uncertainties and biases were studied, concerning biomass estimation (II, III) and to some extent concerning litterfall (IV, V). The uncertainties of this calculation scheme as a whole are reported by Monni et al. (2005) and by Peltoniemi et al. (2005) and further studied within project "Uncertainty assessment of forest carbon balance" (http://www.efi.fi/projects/uncertainty/).

CONCLUSIONS

National GHG inventories concerning forests are needed to fulfil commitments of international climate agreements and moreover, verified carbon sinks can be used partially to offset emissions. Therefore, these inventories should be improved to be more precise and transparent. Biomass stock and stock change estimation could be improved in Finland by using all information that is measured by the NFI at the tree-level. Instead of deducting drain from increment and thereafter converting result to carbon with BEFs, tree-level measurements, like dbh, height, crown base height and upper diameter could be used for biomass estimation connecting destructive biomass measurements conducted by Finnish Forest Research Institute. Modelling of biomass change e.g. with permanent sample plots of NFI could be done with traditional biomass equations (Marklund 1988, Hakkila 1991), using pipe model theory (Valentine et al. 1994)(III) or by connecting biomass to stem surface area (Laasasenaho 1982).

The BEFs developed (I) and tested (II) were found feasible for regional and national biomass estimation. Often BEFs are needed to convert stem volumes to tree biomass, e.g. if tree-level NFI data is not available, GHG inventory agency does not have access to those or increment minus drain approach is used and diameter distribution of drain is not known. We found that foliage biomass estimation with BEFs was not possible for single plots (III).

Therefore, the BEFs can be applied for regional biomass estimation, but not for single stands. These BEFs were based on the biomass sampling of Marklund (1988), and therefore reflect the biomass distribution of trees in Sweden during the 1980s. If our silvicultural or environmental conditions are changing, biomass estimation methods should be updated and applications that account for these changes should be favoured.

Using either tailor-made biomass equations or the approach of Valentine et al. (1994) proved to be optimal for foliage biomass estimation for single plots (III). Since statistically sound destructive sampling of tree biomass is such a laborious and expensive task for a large country such as Finland, alternatives should be sought. Results indicated that the structural correlations of the pipe model theory could be applied for foliage biomass estimation at the plot level (III). Stem biomass is easy to estimate, while the root and canopy biomasses are more challenging; therefore the biomass to sapwood ratios could be used to complete the stem biomass estimates to obtain estimates of the entire tree biomass pool. These ratios of canopy and roots to sapwood could be modelled from all the biomass data gathered and thereafter models for sapwood area at the plot level could be developed. The main advantage of the combination of sapwood and biomass to sapwood models with NFI data relies on the assumption that the prediction error of biomass equations is higher than that of the pipe model approach at the plot level, an assumption that has not yet been tested.

The branch litterfall estimation method presented combines regionally representative datasets of biomass and crown base height measurements (IV, V). The main advantage of this approach is that it uses information from the NFI plots that covers a wide range of forest conditions in southern Finland, and thus results in unbiased estimates for this region. These estimates are affected by the assumptions of the approach, which were that branch litterfall results from crown base height change and that branches are not attached to the stem after they die. Neither of these assumptions holds, especially for Norway spruce which also sheds twigs and branch litter from the inner canopy and has branches attached to the stem long after they die. We may still assume that these estimates for branch litter turnover include the major part of the branch litter and are therefore applicable to the calculation scheme (VI).

We also found that the soil carbon density increased from 6.10 to 6.34 kg C m⁻² during the 82 year study period (VI). On the other hand, we found that in general the soil was a sink of 0.01 kg C m⁻² annually in 1990s, meaning that almost a half of the total increase in soil carbon density was achieved at that time (Figs. 13 and 14). The increasing trend of litter production started from the mid-1980s made soils to be a sink in the 1990s (Figs. 12 and 13). This increasing trend in litter production from living trees results from the increase in tree biomass. To conclude, we showed that both, the tree and soil carbon pools vary heavily on an interannual basis, and even in opposite directions within the same year. Complete counting of carbon pools is therefore needed, especially if forest management is used as a mechanism to create carbon sinks that are credited.

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