Dissertationes Forestales 30

Forest inventory-based large-scale forest biomass and carbon budget assessment: new enhanced methods and use of remote sensing for verification

Petteri Muukkonen

Finnish Forest Research Institute

Department of Geography
Faculty of Science
University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Science of University of Helsinki, for public criticism in Auditorium XII, Main Building, Fabianinkatu 33, on November 17th 2006 at 12 o'clock noon.

Title: Forest inventory-based large-scale forest biomass and carbon budget assessment: new enhanced methods and use of remote sensing for verification

Author: Petteri Muukkonen

Dissertationes Forestales 30

Supervisors: Docent Raisa Mäkipää
Finnish Forest Research Institute

Professor Petri Pellikka
Department of Geography
University of Helsinki

Pre-examiners: Professor Anders Lindroth
Department of Physical Geography and Ecosystems Analysis
Lund University

Associate Professor, Docent, Lars Eklundh
Department of Physical Geography and Ecosystems Analysis
Lund University

Opponent: Professor Pekka Kauppi
Department of Biological and Environmental Sciences
University of Helsinki

ISSN: 1795-7389
ISBN-13: 978-951-651-148-4 (PDF)
ISBN-10: 951-651-148-1 (PDF)

(2006)

Publishers: The Finnish Society of Forest Science
Finnish Forest Research Institute
Faculty of Agriculture and Forestry of the University of Helsinki
Faculty of Forestry of the University of Joensuu

Editorial Office: The Finnish Society of Forest Science
Unioninkatu 40A, FI-00170 Helsinki, Finland
http://www.metla.fi/dissertationes

Muukkonen, Petteri 2006. Forest inventory-based large-scale forest biomass and carbon budget assessment: new enhanced methods and use of remote sensing for verification. University of Helsinki, Department of Geography.

ABSTRACT

In recent years, concern has arisen over the effects of increasing carbon dioxide (CO_2) in the earth's atmosphere due to the burning of fossil fuels. One way to mitigate increase in atmospheric CO_2 concentration and climate change is carbon sequestration to forest vegetation through photosynthesis. Comparable regional scale estimates for the carbon balance of forests are therefore needed for scientific and political purposes.

The aim of the present dissertation was to improve methods for quantifying and verifying inventory-based carbon pool estimates of the boreal forests in the mineral soils. Ongoing forest inventories provide a data based on statistically sounded sampling for estimating the level of carbon stocks and stock changes, but improved modelling tools and comparison of methods are still needed. In this dissertation, the entire inventory-based large-scale forest carbon stock assessment method was presented together with some separate methods for enhancing and comparing it. The enhancement methods presented here include ways to quantify the biomass of understorey vegetation as well as to estimate the litter production of needles and branches. In addition, the optical remote sensing method illustrated in this dissertation can be used to compare with independent data.

The forest inventory-based large-scale carbon stock assessment method demonstrated here provided reliable carbon estimates when compared with independent data. Future activity to improve the accuracy of this method could consist of reducing the uncertainties regarding belowground biomass and litter production as well as the soil compartment.

The methods developed will serve the needs for UNFCCC reporting and the reporting under the Kyoto Protocol. This method is principally intended for analysts or planners interested in quantifying carbon over extensive forest areas.

Keywords: Boreal forests, Carbon balance, Climatic changes, Forest vegetation

ACKNOWLEDGMENTS

This research was conducted as an academic dissertation at the Finnish Forest Research Institute and the Department of Geography of the University of Helsinki. It was carried out under the supervision of Dr. Raisa Mäkipää (Finnish Forest Research Institute) and Professor Petri Pellikka (Department of Geography). I also thank my colleagues from the Finnish Forest Research Institute Dr. Aleksi Lehtonen and Mr. Mikko Peltoniemi for commenting on the original articles.

The warmest thanks go to fellow researchers Dr. Jari Liski (Finnish Environment Institute), Dr. Raisa Mäkipää, Dr Aleksi Lehtonen, Mr. Mikko Peltoniemi (Finnish Forest Research Institute), Mr. Thies Eggers (Department of Engineering, Physics and Mathematics, Mid Sweden University) and Mrs. Taru Palosuo (European Forest Institute) who participated in the coproject *'Integrated method to estimate carbon budgets of forests'*. This project provided the main guidelines for the present work. The endresults and the final conclusions of the project were jointly compiled (**V**).

Dr. Raija Laiho, Dr. Kari Minkkinen, Prof. Harri Vasander (Department of Forest Ecology, University of Helsinki) and Prof. Leena Finér (Finnish Forest Research Institute) provided data on understorey vegetation (**I**). I am also grateful to Mr. Janne Heiskanen (Department of Geography) for his contributions (**VI, VII**).

I would like to thank the Academy of Finland for financing project number 52768 *'Integrated method to estimate carbon budgets of forests'*, which is part of the research programme on the Sustainable Use of Natural Resources (SUNARE). Some parts of the study were also carried out with financial support from the EU-funded research consortium 'Multi-source inventory methods for quantifying carbon stocks and stock changes in European forests' (CarboInvent EKV2-2002-00157) and EU-funded Forest Focus pilot project 'Monitoring changes in the carbon stocks of forest soils'. Thanks also go to the following five Finnish foundations for financial support (**VI**, **VII**) and the present summary: *Marjatta & Eino Kollin säätiö*, *Metsämiesten säätiö*, *Otto A. Malmin lahjoitusrahasto*, *Mikko Kaloisen säätiö* and *Helsingin yliopiston matematiikan ja luonnontieteiden rahasto*.

The Metsähallitus (the state enterprise managing most of the state-owned land in Finland) and the Research Forest Services Unit of the Finnish Forest Research Institute provided the forest stand data used as ground reference data in the (**VI**, **VII**). I would also like to thank the suppliers of the ASTER and MODIS data (the Earth Observing System Data Gateway: http://edcimswww.cr.usgs.gov/pub/imswelcome). I am also grateful to the Finnish National Forest Inventory for providing data on permanent sample plots (**II**) and data on the national tree research (VAPU) programme (**III**, **IV**).

Now it is good time to send some greetings also to my wife Eveliina and my son Topias. Topias, when I have passed this dissertation we can relax and play with your toy railway.

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by five research articles and two submitted manuscripts. The articles are reprinted with kind permission of the publishers.

I	**Muukkonen P.**, Mäkipää R., Laiho R., Minkkinen K., Vasander H. & Finér L. (2006). Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. *Silva Fennica* 40(2): 231–245.
II	**Muukkonen P.** & Mäkipää R. (2006). Empirical biomass models of understorey vegetation in boreal forests according to stand and site attributes. *Boreal Environment Research* (In press).
III	**Muukkonen P.** (2005). Needle biomass turnover rates of Scots pine (*Pinus sylvestris* L.) derived from the needle-shed dynamics. *Trees – Structure and Function* 19(3): 273–279.
IV	**Muukkonen P.** & Lehtonen A. (2004). Needle and branch biomass turnover rates of Norway spruce (*Picea abies*). *Canadian Journal of Forest Research* 34(12): 2517–2527.
V	Liski J., Lehtonen A., Palosuo T., Peltoniemi M., Eggers T., **Muukkonen P.** & Mäkipää R. (2006). Carbon accumulation in Finland's forests 1922–2004 — an estimate obtained by combination of forest inventory data with modelling of biomass, litter and soil. *Annals of Forest Science* (In press).
VI	**Muukkonen P.** & Heiskanen J. (2005). Estimating biomass for boreal forests using ASTER satellite data combined with standwise forest inventory data. *Remote Sensing of Environment* 99(4): 434–447.
VII	**Muukkonen P.** & Heiskanen J. (2006). Biomass estimation over a large area based on standwise forest inventory data, ASTER and MODIS satellite data: a possibility to verify carbon inventories. *Remote Sensing of Environment* (Accepted).

AUTHOR'S CONTRIBUTION

I was responsible for carrying out statistical analyses and for writing of Articles **I**, **II**, and **III** and for analyses concerning needle litterfall modelling and for most of the writing in Article **IV**. In Article **V**, I participated in analyses concerning litter estimation and understorey biomass. In Articles **VI** and **VII**, I was responsible for writing, but data analyses were carried out together with Mr. Janne Heiskanen (Department of Geography, University of Helsinki).

TABLE OF CONTENTS

ABBREVIATIONS

ASTER	Advanced Spaceborne Thermal Emission and Reflection Radiometer
AVHRR	Advanced Very High Resolution Radiometer
BEF	Biomass expansion factor
CLC	Corine Land Cover
COP	Conference of Parties
dbh	Diameter-at-breast height
FAO	Food and Agricultural Organization
IPCC	Intergovernmental Panel on Climate Change
IPCC GPG	Intergovernmental Panel on Climate Change, Good Practice Guidance
LULUCF	Land Use, Land-Use Change and Forestry
LWIR	Longwave infrared spectral region
MODIS	Moderate Resolution Imaging Spectroradiometer
MWIR	Midwave infrared
NBP	Net biome productivity which was calculated by subtracting felled roundwood removed from the forests (RE) from NEP. $NBP = NEP - RE$
NEP	Net ecosystem productivity which was obtained by subtracting heterotrophic respiration R_h from NPP. $NEP = NPP - R_h$
NFI	National Forest Inventory
NIR	Near-infrared spectral region
NPP	Net primary productivity which was calculated by summing up the change in growing stock of trees ΔGS, change in the biomass of understorey vegetation ΔB, litter production of trees and understorey L, natural losses (mortality) of trees M and fellings of trees by humans (harvesting) F. $NPP = \Delta GS + \Delta B + L + M + F$.
NOAA AVHRR	National Oceanic and Atmospheric Administration, Advanced Very High Resolution Radiometer
SOM	Soil organic matter
SPOT	Satellite Probatoire d’Observation de la Terre

SWIR/MWIR	Shortwave and midwave infrared spectral region
TIR	Thermal infrared spectral region
UNFCCC	United Nations Framework Convention on Climate Change
VAPU	National tree research programme
VIS	Visible light spectral region
VNIR	Visible and near infrared spectral region
YASSO	Soil model Yasso

1 INTRODUCTION

1.1 Requirements for assessment of forest carbon balance

Climate change is recognized as a major potential threat to the world's environment and to economic development. Carbon sequestration by terrestrial ecosystems is important in the global carbon balance, hence for limiting the concentration of CO_2 in the atmosphere. Carbon research has become a focal topic in science since the observed increase in levels of atmospheric CO_2 (from ~280 ppm in 1800 to ~315 ppm in 1957 to ~356 ppm 1993) and, more recently, because there are two key policy-related reasons for measuring carbon in forests. Firstly, commitments under the UNFCCC signing of the Climate Convention United Nations Framework Convention on Climate Change (UNFCCC) has forced nations to assess their contributions to the sources and sinks of CO_2 and to evaluate the processes that control CO_2 accumulation in the atmosphere (Schimel 1995). The UNFCCC, signed by more than 150 countries, requires that all parties to the Convention commit themselves to develop, periodically update, publish and make available to the Conference of Parties (COP) their national inventories of emissions by sources and removals by sinks of all greenhouse gases, using comparable methods. Secondly, the recognition that forestry activities could be both sources and sinks of carbon led to their inclusion in the Kyoto Protocol (Brown 2002).

Forest vegetation and soil may act as significant sinks or sources of atmospheric CO_2, depending on land use, forest management and environmental conditions. Plants acquire C, in the form of CO_2 from the atmosphere through the stomata of their leaves and incorporate it into the organic matter of their own biomass through the process of photosynthesis. Respiration by all organisms returns CO_2 to the atmosphere. The living forests themselves are carbon pools and will be sinks as long as the trees are growing. Boreal forests, which occupy much of the circumpolar region between 50° and 70° N (Ahti et al. 1968), are of particular interest because, among all the biomass, they may undergo the greatest climatically induced changes (Bonan et al. 1992, Myneni et al. 1997, IPCC 2001). In addition, during recent decades terrestrial ecosystems in the boreal forests of the Northern Hemisphere appear to have accounted for a major portion of the terrestrial sink, partly as a result of improved forest management (Liski et al. 2003b, Ståhl et al. 2004). However, predicting boreal carbon budgets for large continental areas is complex because the landscape is highly diverse and plant biomass is very variable on spatial and temporal scales (Ciais et al. 2000). Extensive natural disturbances and harvestings by humans may also occur.

The need for reporting carbon budgets (example of pools and fluxes that are essential as a part of forest carbon budget are given in Figure 1) for the Kyoto Protocol has placed additional demands for reliable surveying methods that are verifiable, specific in time and space, and cover large areas at acceptable cost (Krankina et al. 2004, Patenaude et al. 2005). When methods for assessing carbon pools in boreal forests are considered it is usually appropriate to make use of the data available from the national forest inventory (NFI) (Baritz and Strich 2000, Hall et al. 2001, Banfield et al. 2002, Brown 2002, Mickler et al. 2002, Turner et al. 2004). In Finland, the NFI is a good source of information on state and change in forest resources, including carbon pools (Tomppo 2000). Forest inventory data may consist of both field measurements and remote sensing data, although soil carbon estimates are not normally provided and covered by traditional NFIs.

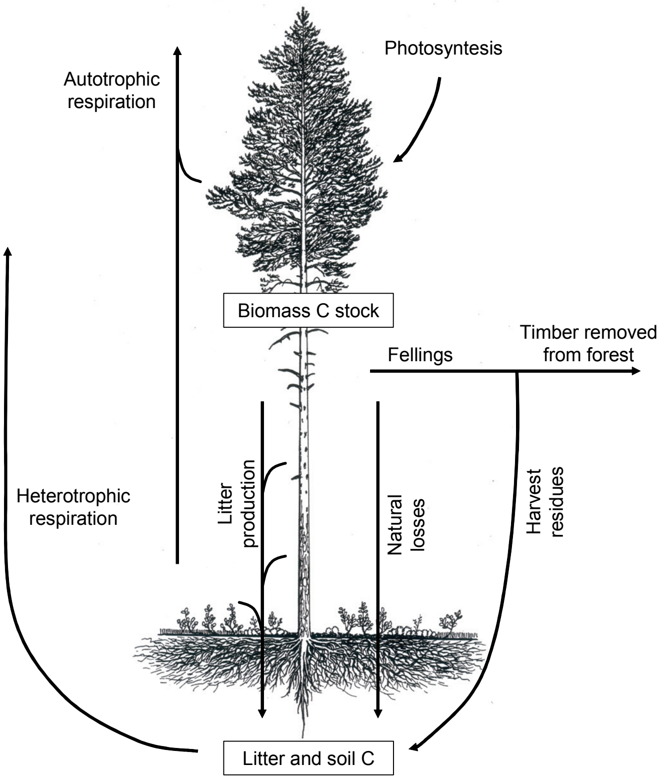

Figure 1. An example of carbon pools (boxes) and gas and material fluxes (arrows) in a forest ecosystem (**V**).

1.2 Forest inventory-based large-scale carbon budget assessment

1.2.1 General

Methods for carbon stock change assessment involve measuring the difference in carbon stocks between two points in time or estimating the difference between gross growth and removals (Turner et al. 2004). For existing forests, NFI data are the most practical means for estimating the carbon content of forests, since the data are generally collected at the required scales and from the population of interest in a statistically well-designed manner (Brown 2002). An inventory-based approach can be used to cover large land areas and a variety of species and site conditions. This approach can also be based upon existing forest inventory networks such as the Finnish NFI. Ciais et al. (2005) showed that the advantages of using NFIs lie in covering and understanding spatial variability at the expense of detailed knowledge of the component processes.

Traditional forest inventories provide information on stand volumes, but not on biomass or carbon stock (FAO 2000). Thus, the available volume estimates had to be converted into biomass and carbon budget estimates. Data from these inventories can be converted to biomass and therefore to the carbon in one of two ways, depending upon the level of detail reported (Brown 2002). The relationship between biomass and stand volume makes it possible to estimate forest tree biomass at the national level from NFI data that are readily available in most countries or regions (Fang et al. 1998, FAO 2000).

In contrast, general methods for estimating the carbon balances of nonliving organic matter pools are still lacking. Quantifying the carbon balances of litter and soil organic matter (SOM) is particularly complicated since the expected changes are extremely low (Liski et al. 2002, Peltoniemi et al. 2004). Even the spatial variability at a forest site may be several times greater than the changes expected over a decade (see Liski 1995). For this reason, various modelling approaches have been applied to obtain stock change estimates of litter and soil carbon (Kurz and Apps 1999, Heath et al. 2002, Liski et al. 2002). The diversity of these methods makes the comparison of the results difficult (Goodale et al. 2002).

1.2.2 Role of understorey vegetation

The carbon budgets of trees and forest soil have been modelled extensively, but understorey vegetation is not usually included in these analyses (Bonan et al. 1992, Liski et al. 2002, Nabuurs et al. 2003). In comparison to other components of forest ecosystems, the biomass of understorey vegetation is considered to be small and is sometimes dismissed as negligible (e.g. Ståhl et al. 2004). Pussinen et al. (1997) showed that, over 50% of the carbon stock in boreal forests may be in trees, one third in SOM and about 10% in litter. The proportion of the total forest carbon stock stored in understorey vegetation is only 1–2% (Lakida et al. 1996, Pussinen et al. 1997), but disturbances or exceptional conditions may introduce wide variation. However, the biomass of understorey vegetation may play an important role in many ecosystem processes, e.g. in the nutrient and carbon cycle (Yarie 1980, Van Cleve and Alexander 1981), due to rapid turnover at the biomass level and the presence of easily decomposable litter (Zavitkovski 1976, Chapin 1983, Tappeiner 1989). In upland soils, the annual litter production of understorey vegetation may represent a considerable proportion of the total litter production, varying from 4% to 30% (Hughes 1971). Studies ignoring understorey vegetation (e.g. Kurz and Apps 1999, Nabuurs et al. 2003) may result in underestimation of the NPP (net primary productivity) and litter production and, in addition, the carbon stock and sink of soil that are dependent on the total litter production.

1.2.3 Litter production and its reliable estimation

Litterfall represents the most important source of elemental flux to the forest floor. The litter pool usually refers to the dead organic debris that is supplied to the soil by litterfall and as root litter (Ståhl et al. 2004). During the life of the forest, the litter pool continuously receives carbon from the forest in the form of dead foliage, roots, branches and whole trees as well as dead parts of the understorey vegetation (Cannel and Milne 1995). In the present study, the litter already fallen to the ground is handled as part of the soil organic layer, which is part of the soil carbon pool.

The proportion of aboveground litter compartments of Norway spruce (*Picea abies* (L.) Karst.) is nearly 73% for needles, 13% for branches, 5% for cones and 10% for other mixed litter (Viro 1955), which consists of seed, flowers, bud scales, epiphytic lichen and small pieces of bark. The percentage of litter compartments of Scots pine (*Pinus sylvestris* L.) is nearly 67–85% for needles, 7–12% for branches, 4–11% for bark, 0.5–2% for cones and 2–6% for other mixed litter (Viro 1955, Mälkönen 1974). Mixed litter consists of seed, flowers, bud scales and epiphytic lichen. Although the amount of branch litterfall is much lower than that of foliage litter, its contribution to the carbon stock of the soil is high since it decomposes slowly; this should be taken into account when ecosystem models are built.

1.2.4 Remote sensing in carbon estimation

The purpose of comparing national carbon inventories and to improve their quality is to establish their reliability and to check the accuracy of the numbers reported by independent means (IPCC 2003). There are many approaches that can be used to verify carbon estimates. An overall comparison exercise may include cross-checking of the results at different geographical scales. IPCC good practice guidance (GPG) (IPCC 2003) states that remote sensing methods are especially suitable for comparing the national land use, land-use change, and forestry (LULUCF) carbon pool estimates, especially the aboveground biomass, provided that adequate ground reference data (not used for the carbon stock inventory itself) are available to represent the range in forest biomes and management regimes for which estimates are required. In addition, measurements of greenhouse gas fluxes at ecosystem scales may be used to compare, at local scales, the changes reported in carbon stock (IPCC 2003). These flux observations are usually carried out by micrometeorological techniques, such as eddy covariance, using canopy towers placed inside forests or other ecosystems, mainly for CO_2 exchange measurements (Aubinet et al. 2000). Even if the carbon fluxes can be measured precisely for a single stand by the eddy-covariance method, it is still not practical to have a sufficient number of systems so that scaling up to the national level becomes meaningful (Ståhl et al. 2004).

When the utilization of remote sensing based methods for biomass and thus carbon estimation is considered, the purposes for which the methods will be used should be identified. Most countries may have NFIs providing relatively reliable estimates for large areas. If the frequency of the NFIs is not high enough, medium- or coarse-resolution remote sensing data can be used. Tomppo et al. (2002) concluded that the benefits of using such remote sensing data may be: 1) frequent coverage repetition, 2) easy coverage of large areas, 3) extrapolation of estimates to areas with no ground reference data and 4) low price per area covered.

Future direct measurements of carbon stock in boreal forests may also rely on remote sensing data, and new remote sensing data collection technologies are in development (Brown 2002). Although biomass cannot be directly measured from space, remotely sensed reflectance can be related to biomass estimates based on field measurements (Dong et al. 2003). Yet, it must be born in mind that the relationship between biomass and canopy reflectance is largely contextual (Patenaude et al. 2005). This reflects the inherent difficulty in using optical remote sensing data for monitoring forest biomass.

A wide range of approaches has been proposed for quantifying biomass using optical and radar remote sensing systems, although no studies have yet presented a technique that is consistent, reproducible and applicable at regional or continental scales (Rosenqvist et al. 2003). The imaging data used should be chosen according to the geographical scale of the target area and desired degree of resolution (IPCC 2003). At global-level mapping, coarse- and medium-resolution optical sensors, such as the National Oceanographic and Atmospheric Administration Advanced very High Resolution Radiometer (NOAA AVHRR) (e.g. Häme et al. 1997, Dong et al. 2003) and the Moderate Resolution Imaging Spectrometer (MODIS) (Baccini et al. 2004, Xia et al. 2005, **VII**), are most useful due to their frequent temporal coverage, although for quantifying change at local to regional levels, data provided by finer resolution instruments, such as Landsat (e.g. Häme et al. 1996, Fazakas et al.

1999, Tomppo et al. 2002, Krankina et al. 2004, Turner et al. 2004), the Advanced Spaceborn Thermal Emission and Reflection Radiometer (ASTER) (**VI**) and the Satellite Probatoire d'Observation de la Terre (SPOT) sensors are required. Also the mapping of forest biomass using radar was also recently explored (Rauste et al. 1994, Tomppo et al. 2002, Gaveau et al. 2003, Rauste 2005, Rauste 2006), but in this dissertation I have only focused on optical remote sensing and on its role in biomass estimation.

1.3 Objective

The aim of this dissertation was to improve methods for quantifying and verifying inventory-based carbon pool estimates for the boreal forests on mineral soils. Ongoing forest inventories provide a statistical basis for estimating the levels of carbon stocks and stock changes, but new enhanced methods are still needed. The methods developed will serve the needs for UNFCCC reporting and the reporting under the Kyoto Protocol.

In this dissertation, I demonstrate the inventory-based carbon budget assessment as well as new enchanced methods in it. Those enhanced methods deals with biomass estimation of understorey vegetation and litter estimation of needles and branches. I also show the possibility to use optical remote sensing methods to verify large-scale forest biomass estimates.

2 MATERIAL

2.1 Field data

2.1.1 National Forest Inventory

The calculation method for large-scale forest carbon budget assessments (**V**) is based on the NFI data. The NFI has been conducted in Finland nine times so far, each requiring from 3 to 9 years to survey the whole country. The first NFI in 1921–1924 was a line transect survey with the length of the surveyed line totalling more than 13 000 km and the distance between the survey lines being 26 km (Ilvessalo 1927), whereas the last completed NFI applied systematic cluster sampling and took measurements at about 70 000 sites (Tomppo 2000). Traditionally, the most important target variables of forest inventories have been forest area, growing stock and increment, all of which must be converted to satisfy the requirements of carbon inventories.

*2.1.2 Understorey vegetation data (**I, II**)*

2.1.2.1 Relationship between biomass and percentage cover (**I**)

The data used in Article **I** (see Table 1) to study the relationship between biomass and percentage cover of plants of understorey vegetation was compiled from several sources, with differences in the details of the sampling procedures. In each study the percentage cover was estimated visually. The biomass of the aboveground parts was measured either as single species or as species groups such as herbs and grasses, dwarf shrubs, lichens and mosses. In some cases, the biomass was measured separately only for the bottom and field layers. A total of 225 sample quadrats were located in the upland soils and 195 on the peatlands. The exact sampling procedures for each stand are presented in the corresponding publications. In general, they resulted in comparable observations of the aboveground biomass of the understorey vegetation in mineral soils and on peatlands in Finland.

2.1.2.2 Understorey vegetation according to stand and site attributes (**II**)

The biomass models of understorey vegetation followed the stand and site attributes developed (**II**) which in turn were based on the biomass/cover equations (**I**) and on the nationwide vegetation data from a systematic network of permanent sample plots (300 m^2) established by the NFI in 1985–1986. The sample plots form a regular network of clusters; in southern Finland each cluster consists of four plots at 400-m intervals and in northern Finland three plots at 600-m intervals. In the south there is one cluster per area of 16 km × 16 km and in the north one cluster per area of 24 km × 32 km. Only sample plots with the required forest site attributes were included. Of 3009 sample plots covering the whole of Finland, a total of 1667 located in upland soils and 592 located on peatlands were selected for our study. The percentage cover of plants was estimated visually on 2-m^2 quadrats located systematically within the plots (see Mäkipää and Heikkinen (2003) for further details). Each quadrat was used as an individual observation in further analyses.

The aboveground biomass of understorey vegetation was calculated for the following species groups: herbs and grasses, mosses, lichens, and dwarf shrubs. The biomasses were estimated by species group since, despite the relatively wide variability in floral composition, the dense cover and the large number of species, the ground cover in the upland soils of boreal forests is dominated by only a few species regardless of the phase of stand development (Kubícek and Simonovic 1982, Havas and Kubin 1983, Kubin 1983, Reinikainen et al. 2001). In general, the dominant and subdominant species represent 85–97% of the total ground biomass (Kubícek and Simonovic 1982).

Table 1. Field and optical remote sensing data used in original articles.

Article	
I	Compiled data of aboveground biomass and percentage cover of understorey vegetation (for comprehensive list see Article **I**)
II	Nation-wide vegetation data from a systematic network of permanent sample plots established by the Finnish NFI in 1985–1986
III, IV	National tree research data (VAPU) established by the Finnish Forest Research Institute
V	Forest inventory data on forest area and stand volume established by Finnish NFI 1922–2002
VI	Two standwise forest inventory datasets; the statistical models were constructed using one field dataset (provided by Metsähallitus) and evaluated by another (provided by Finnish Forest Research Institute)
	ASTER satellite data
VII	MODIS satellite data

Stand age, basal area, stem volume, stem number, fertility class, coordinates, elevation and effective temperature sum were recorded or derived for each stand by NFI. The effective temperature sum (sum of daily mean temperatures, threshold value +5 °C) was estimated for each site using the surface-fitting model of Ojansuu and Henttonen (1983), which is based on measurements of monthly mean temperature recorded at the Finnish Meteorological Institute weather stations. Stand age was estimated using increment cores from a single sample tree that represented the dominant canopy layer. The basal area was estimated as an average of three relascope observations. The fertility levels of the stands were estimated by a botanist, based on the levels found in the understorey vegetation.

*2.1.3 Needle litterfall data (**III, IV**)*

The national tree research data (VAPU) used (**III**, **IV**) consisted of measurements of sample trees on sample plots established by the Finnish Forest Research Institute in southern Finland (south of 62°4' latitude) during 1988–1990. Three to five sample trees (with diameter-at-breast height (dbh) more than 5 cm) from the dominant canopy layer closest to the plot centre were selected and felled (Figure 2). A total of 64 Scots pine and 80 Norway spruce trees were used.

Estimation of needle litterfall is based on needle cohort longevity (VAPU database). First-order needle cohorts (Figure 3) were estimated visually from two branches in the 15th whorl from the top of the tree (Figure 2a). The first branch pointed to the centre of the sample plot and the second pointed in the opposite direction (Figure 2b). Kendall’s coefficient of concordance (Ranta et al. 1999) shows that there were statistically significant similarities between the needle cohorts of the two measured directions. Therefore, to avoid measurements that are dependent on each other, it is reasonable to analyse the measurements of branches in only one direction. The percentage survival of needles in each of the needle cohorts was estimated visually and classified into one of six classes: 1) 0–5%, 2) 6–25%, 3) 26–50%, 4) 51–75%, 5) 76–95% and 6) 96–100%.

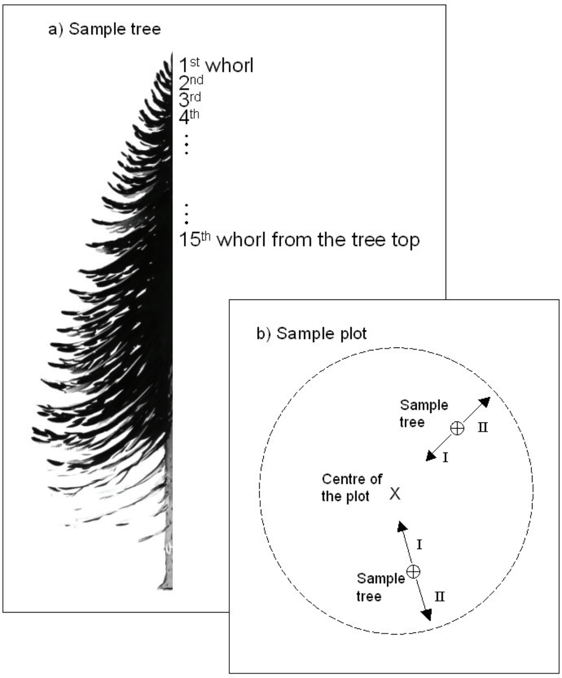

Figure 2. Sampling of the needle cohorts was estimated visually from the two branches in the 15th whorl (**a**). The first branch pointed to the centre of the sample plot and the second pointed in the opposite direction (**b**). The single sample tree is presented in (**a**) and the sample plot in (**b**).

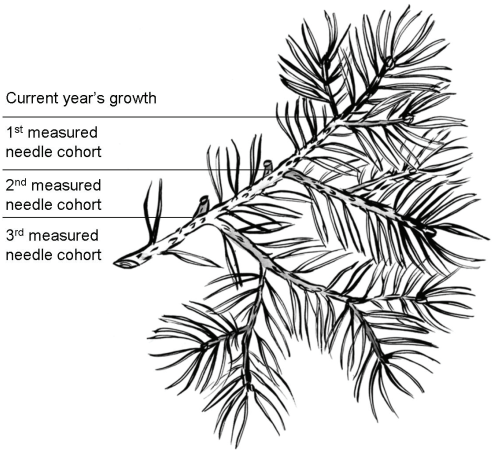

Figure 3. Needle cohorts. First-order needle cohorts are located on the main stalk of the branch.

*2.1.4 Ground reference data for remote sensing (**VI**)*

The study area (**VI**) is located in southern Finland (Figure 4). In this study, two standwise forest inventory datasets were used as ground reference data. The statistical models were constructed using one field dataset (Evo) and evaluated by another (Vesijako). The Evo data was provided by the Metsähallitus, which is a state enterprise operating within the administrative sector of the Ministry of Agriculture and Forestry, and it manages most of the state-owned land and waters in Finland. The Vesijako data were provided by the Finnish Forest Research Institute. Both forest stand datasets included stand volume and stand age, which were transformed to aboveground biomass of trees and understory vegetation (t ha^{-1}). The aboveground tree biomass by tree component (total aboveground, stem, foliage, branches) was derived from the stand volume, using specieswise age-dependent biomass expansion factors BEFs (Lehtonen et al. 2004). The aboveground biomass of understory vegetation by species group was derived according to the stand age and dominant tree species (**II**). Only forest stands in mineral soils were examined. The number of forest stands included was 1331 and 679 in the modelling (Evo) and validation (Vesijako) datasets, respectively.

2.2 Optical remote sensing data

ASTER is a high-spatial resolution multispectral imager with three subsystems operating in different spectral regions, namely the visible and near infrared (VNIR), the shortwave infrared (SWIR) and the thermal infrared (TIR) (Yamaguchi et al. 1998). The spatial resolution is 15, 30 and 90 m for VNIR, SWIR and TIR, respectively. A single ASTER image covers an area of 60 × 60 km^2. In this study, the red and NIR spectral bands were used (Table 2).

Table 2. Spatial resolution and spectral overlap of ASTER and MODIS data used (Ardanuy et al. 1991, Masuoka et al. 1998, Yamaguchi et al. 1998).

	ASTER	MODIS
Spectral range (µm)	Band 2: 0.63–0.69, Red	Band 1: 0.62–0.67, Red
	Band 3: 0.76–0.86, NIR	Band 2: 0.841–0.876, NIR
Spatial resolution (m)	15	250

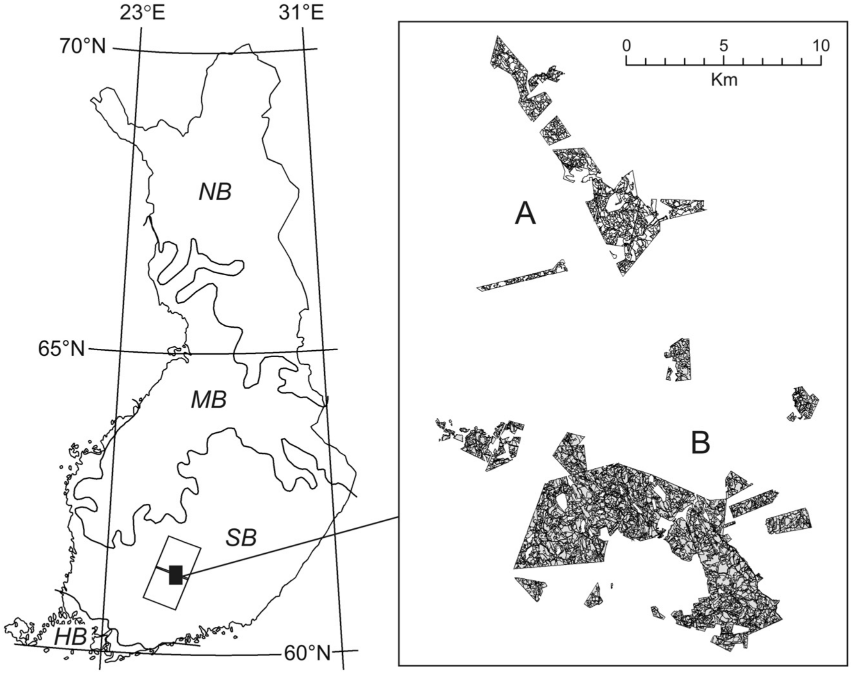

Figure 4. Location of the study area and coverage of the ASTER images and the forest stand maps employed. **A** corresponds to the Vesijako dataset used in training and **B** to the Evo dataset used in validation. Following division of the vegetation zones in Finland, the study area is situated in the southern Boreal Zone (SB) (Ahti et al. 1968, p. 188). The other vegetation zones are the Hemiboreal (HB), Mid-Boreal (MB) and Northern Boreal (NB).

The MODIS instrument provides 36 spectral bands ranging in wavelength from 0.46 µm to 14.4 µm (Ardanuy et al. 1991, Masuoka et al. 1998). MODIS has four refractive objective assemblies, one for each of the visible (VIS), near-infrared (NIR), shortwave and midwave infrared (SWIR/MWIR) and longwave infrared (LWIR) spectral regions (Ardanuy et al. 1991). Two bands are imaged at a nominal resolution of 250 m at nadir (bands 1–2), with five bands at 500 m (bands 3–7), and the remaining 29 bands at 1 km (bands 8–36). The swath dimensions are 2330 km (across the track) by 10 km (along the track at nadir). These two imager instruments, ASTER and MODIS, were carried onboard the Terra spacecraft (Earth Observing System AM) on December 18, 1999. We used MODLAND product MOD09 to provide surface reflectance data (Justice et al. 2002).

MODIS spectral bands 1 and 2, covering almost the same wavelength area as ASTER bands 2 and 3 (Table 2, Figure 5), were calibrated using regression analysis (Häme et al. 1997). The following linear models were used:

$$ASTER_{(\mathrm{RED})} = \beta_0 + \beta_1 \cdot MODIS_{(\mathrm{RED})} \tag{1}$$

$$ASTER_{(\mathrm{NIR})} = \beta_0 + \beta_1 \cdot MODIS_{(\mathrm{NIR})} \tag{2}$$

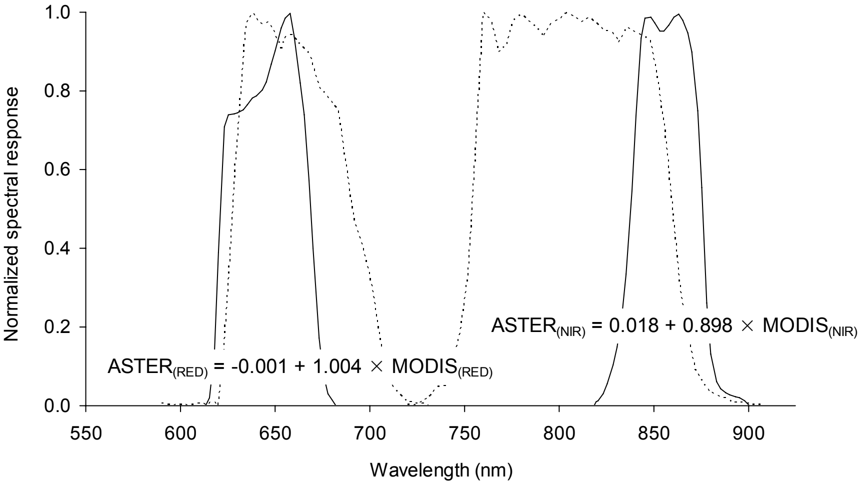

Figure 5. The normalized spectral response of red and NIR ASTER and MODIS bands. Dashed lines correspond to the ASTER bands 2 and 3 and solid lines to the MODIS bands 1 and 2. The linear models were used for calibrating bandwidth differences.

The terms β_0 and β_1 of these linear models were calculated from Curran and Hay (1986) and Cohen et al. (Cohen et al. 2003):

$$\beta_0 = \frac{\sigma(ASTER_{(i)})}{\sigma(MODIS_{(j)})}, \tag{3}$$

$$\beta_1 = \overline{ASTER_{(i)}} - a \cdot \overline{MODIS_{(j)}}, \tag{4}$$

where $\overline{ASTER_{(i)}}$ and $\overline{MODIS_{(j)}}$ are the means of the variables ASTER and MODIS and, $\sigma(ASTER_{(i)})$ and $\sigma(MODIS_{(j)})$ the standard deviations. The parameterizations of the linear models are based on the overlay of ASTER and MODIS data for all pixels in the study area.

3 DATA ANALYSIS

3.1 Forest inventory-based large-scale carbon budget assessment (V)

3.1.1 Computational scheme

In this study, the computational scheme of the forest carbon budget (Figure 6) is based on forest inventory data on forest area and stand volume (**V**). The carbon pools (living vegetation and soil) and their annual changes (1922–2004) were estimated from the forest inventory data with the aid of modelling. The basic concepts of this calculation method have been presented earlier (Liski et al. 2002), but here a more advanced version of the method is demonstrated. The enhanced method consists of new models shown to be appropriate for regional and national scale inventories.

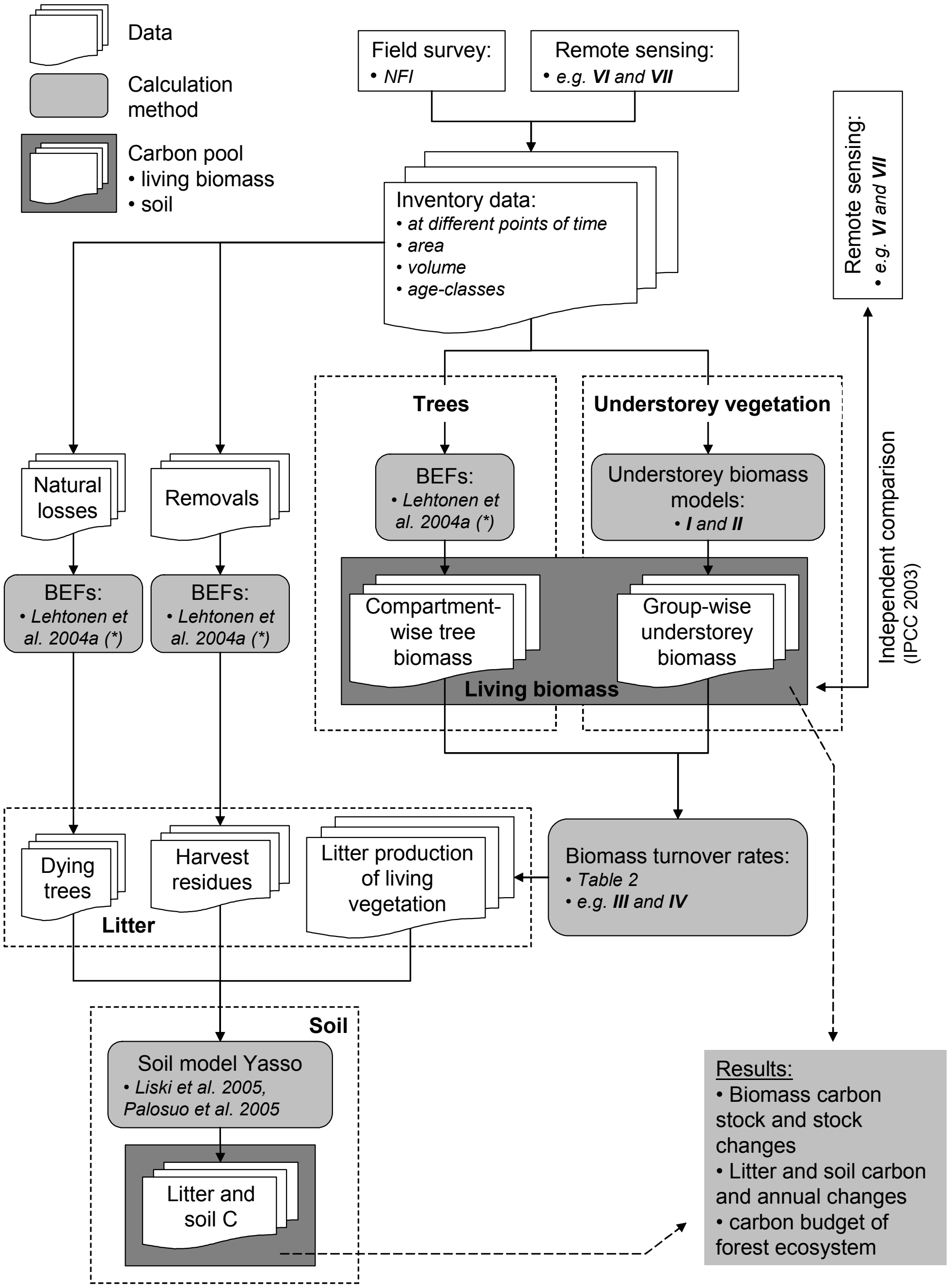

Figure 6. Computational scheme. In biomass estimation of trees (*) there are few exceptions (see Chapter 3.1.2). For uncertainty of different components and factors see Peltoniemi et al. (2006).

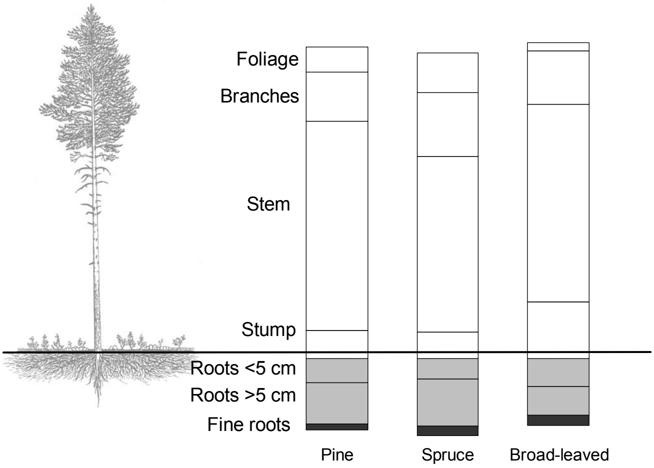

Figure 7. Relative distribution of tree biomass – averages for Finland (**V**).

3.1.2 Tree biomass

In the present study, estimates for the volume of growing stock were converted to biomass, using species-specific BEFs for different biomass compartments (for distribution of the tree biomass see Figure 7) (Lehtonen et al. 2004a). The tree biomass is normally divided in to the aboveground parts stem, bark, branches, foliage, and the belowground parts stump and roots (Lehtonen et al. 2004a, Ståhl et al. 2004). Suitable BEFs were not available for foliage of broad-leaved trees, the biomass of which was assumed to be proportional to branch biomass, and the proportion to decrease from 80% to 20% with increasing stand age of 10 to 150 years.

Suitable BEFs were not available for estimating the biomass of fine roots, coarse roots and stumps of broad-leaved trees (Lehtonen et al. 2004a). To estimate the biomasses of these compartments, the fine root biomass of conifers was estimated to be proportional to foliage biomass (**V**). For broad-leaved forests, the ratio between fine root and stem biomass was assumed to be the same as in pine forests of the same age. The compounded biomass of stump and transportation roots was assumed to be 53% of the stem biomass in broad-leaved forests (Laitakari 1935), and this biomass was divided equally between these components.

3.1.3 Litter production of trees

In the present study, the computational method distinguished three carbon fluxes to litter and soil: 1) the litter production of living vegetation resulting from biomass turnover, 2) mortality of tree individuals due to natural causes and 3) residues of harvests (see Figure 8) (**V**).

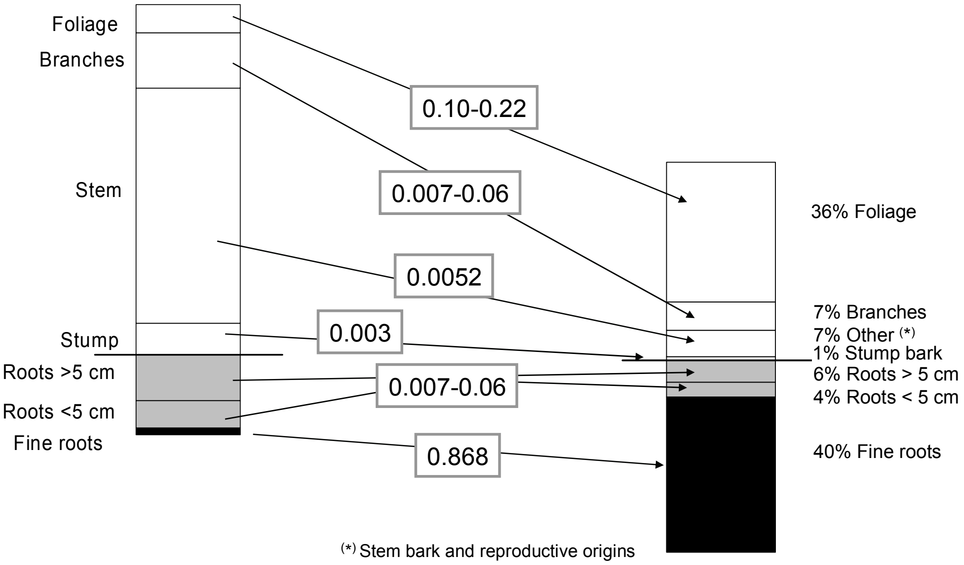

Figure 8. Litter production of pine forests – averages for Finland (**V**). The biomass of each tree compartment was multiplied by the compartmentwise biomass turnover rate. For biomass turnover rates see Table 3.

There are two approaches to estimate litter production in living vegetation. Firstly, the average values of litterfall measurements can be used, utilizing either litterfall measurements from the study area or litterfall modelled according to site conditions (e.g. Berg and Meentemeyer 2001, Starr et al. 2005). Secondly, the time series of litterfall from living vegetation, $l_j(t)$, can be calculated for each biomass compartment by multiplying the biomass of the growing stock, $m_i(t)$, by the component-specific biomass turnover rates, r_i (Liski et al. 2002, Masera et al. 2003):

$$l_i(t) = r_i m_i . \tag{5}$$

In the present study, the latter approach was used to estimate the litter produced by living vegetation (see the computational scheme in Figure 6) (for biomass turnover rates see Table 3). The natural mortality was taken to be equal to the biomass of dying trees. The harvest residues were assumed to be equal to the biomass of felled trees, excluding 91% of the stem biomass that was removed from the forests.

Table 3. Biomass turnover rates (per year) used to estimate the litter production of trees and ground vegetation (**V**).

	Trees					
	Spruce forests		Pine forests		Broad-leaved forests	
	S[a]	N[b]	S	N	S	N
Foliage	0.10[c]	0.05[c]	0.22[d]	0.10[d]	0.78[e]	
Branches & roots	0.0125[c]		f(t)[f]		0.0135[g]	
Stump bark	0.0[h]		0.0030[i]		0.0001[j]	
Reproductive origins & stem bark	0.0027[h]		0.0052[i]		0.0029[j]	
Fine roots	0.811[k]		0.868[l]		1.0[m]	

	Ground vegetation
Mosses	0.33[n]
Lichens	0.1[o]
Dwarf shrubs, aboveground	0.25[p]
Herbs & grasses, aboveground	1.0[q]
Dwarf shrubs, belowground	0.33[r]
Herbs & grasses, belowground	0.33[r]

---

[a] Southern Finland

[b] Northern Finland

[c] **IV**

[d] **III**

[e] Leaves of broad-leaved trees became 22% lighter during yellowing process in autumn (Viro 1955)

[f] As a function of age (Lehtonen et al. 2004b)

[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)

[l] (Kurz et al. 1996)

[m] We assumed that broad-leaved 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)

[o] 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)

3.1.3.1 Analysis for estimating litter production of needles (**III**, **IV**)

To study needle-shed dynamics and to estimate the turnover rate of needle biomass, ordinal regression (Bender and Benner 2000) was used to model the relationship between age of the needle cohort and the survival class. The survival classes, according to the age of the needle cohort, characterized the decrease in needle density over time. In other words, the needle survival classes indicate the proportion of original needles present in a needle cohort at a particular time.

The dry weight of living needles increases during the first four years (Viro 1955). The weight of second-year, third-year and older needles is 36%, 30% and 40%, respectively, higher than that of first-year needles. Norway spruce shed needles from all needle cohorts and most of the needles become yellow before they are shed (Salemaa et al. 1993). Upon yellowing, the spruce needles become lighter and the absolute amounts of nutrients in them usually diminish, being transferred to the trunk (Viro 1955). In other words, a substantial amount of the nutrients required for construction of new needles each year can be supplied by the relocation of nutrients from aging needles (Schoettle and Fahey 1994). In this process spruce needles lose 13–39% of their weight, depending on the age of the needle cohort (Viro 1955).

The biomass turnover rate of needles (r_f) in the timeperiod approach was calculated with the following model as

$$r_f = \frac{\sum_{i=0}^{n-1}(b_i - b_{i+1}) \cdot w_i \cdot d_i}{\sum_{i=0}^{n-1}(b_i \cdot w_i)}, \tag{6}$$

where b is the percentage survival of the needle cohort, w is a weight factor indicating weighting of needles over time and d is loss of weight during yellowing of needles (**III**, **IV**). The numerator indicates the total number of needles removed annually and the denominator the total number of needles on a tree or single branch. In the present study, n is 6 or 12, which indicates the number of needle age-classes in Scots pine and Norway spruce trees, respectively.

3.1.4 Understorey vegetation

The biomass of the understorey vegetation was estimated using regression models that give the biomasses of various species groups based on stand age (**II**). These regression models (**II**) were based on biomass/cover equations (**I**) and on the vegetation data of a systematic network of permanent sample plots established by the Finnish NFI (Chapters 3.1.4.1 and 3.1.4.2 show how these models were developed). Understorey vegetation may include herbaceous species, grasses, dwarf shrubs, mosses, and lichens (Zavitkovski 1976, Ford and Newbould 1977). This definition, which was also applied here, excludes tall shrubs and epiphytes. In boreal forests, this exclusion results in only minor underestimates of the biomass of understorey vegetation. The bottom layer consists of mosses and lichens only, whereas the field layer includes dwarf shrubs, herbs, and grasses. Dwarf shrubs are low shrubs with perennial aboveground woody stems that are situated near the ground surface. In the present study, young tree saplings were also considered dwarf shrubs. Herbs and grasses are annual plants without perennial aboveground woody stems. The divisions are based on a traditional *a priori* grouping, which is typically defined by discrete and measurable biological trait differences (Reich et al. 2003).

In any season, the biomass of the belowground parts of the understorey vegetation is substantially higher than that of the aboveground parts (Zavitkovski 1976, Kubícek and Simonovic 1982, Kubícek et al. 1994). The biomass models of understorey vegetation developed (**II**) consider aboveground biomass only. The proportion of the biomass of the field layer vegetation located in the belowground parts was estimated to be about 70% of the total biomass (Mälkönen 1974, Perina and Kvet 1975, Kubícek and Simonovic 1982, Havas and Kubin 1983, Kubícek et al. 1994, Palviainen et al. 2005a).

3.1.4.1 Analysis for examining relationship between biomass and percentage cover (**I**)

The hierarchical structure (i.e. sample quadrats within stands) in the data implies a lack of independence among measurements (Fox et al. 2001). Correspondingly, mixed models that accounted for variance deriving from the different hierarchical levels in the data were used.

The aboveground biomasses (y) of mosses and lichens in upland soils as well as those of the field and bottom layers on peatlands were modelled as a function of percentage cover (x) with a mixed nonlinear model

$$y_i = \frac{u + x^2}{(\beta_0 + \beta_1 \cdot x)^2} + \varepsilon \,, \tag{7}$$

where β_0 and β_1 are fixed population parameters and u is a random parameter. The aboveground biomasses of dwarf shrubs and herbs/grasses in upland soils were modelled with a mixed linear model

$$y_i = \beta_1 \cdot x + u + \varepsilon \,. \tag{8}$$

Several model structures were tested and compared with the fit-statistics and with the visual examination. Since the species composition may change with the change in total abundance of the species group, both linear and curvilinear relationships between cover and biomass were tested. The final decision between use of the nonlinear and linear models was made, based on both evaluation of the differences between these two models and the ecological aspects of the current species group.

3.1.4.2 Analysis for examining biomass of understorey vegetation according to site attributes (**II**)

The aboveground biomasses (y) of the species groups (i) of the understorey vegetation were modelled with the mixed model according to forest stand and site attributes. Mixed models accounting for variance derived from different hierarchical levels in the data were used, since the sample quadrats could not be treated as independent units (Fox et al. 2001). In the mixed model

$$\sqrt{y_i + 0.5} = u + \beta_0 + \beta_1 a_1 + \ldots + \beta_k a_k + \varepsilon \,, \tag{9}$$

u is a mixed parameter and ε is an error term. The terms $a_1 - a_k$ are functions of measured forest attributes $z_1 - z_k$; $a = f(z_j,\ j = 1, 2, ..., k)$, which are derived by the simple interactions $a = z_1$, by the two-way interactions $a = z_1 \cdot z_2$, or by the quadratic interactions $a = z_1^2$. The square-root transformation was used to obtain absolute prediction values. In addition, the

$$\sqrt{y_i + 0.5} \tag{10}$$

transformation was used instead of the

$$\sqrt{y_i} \tag{11}$$

transformation, since the dependent variables also contained zero values (Ranta et al. 1999).

3.1.5 Modelling soil carbon

Soil organic carbon refers to a mixture of dead plant residues in various stages of decomposition and of substances synthesized microbially or chemically from the breakdown products (Ståhl et al. 2004). In the present dissertation, soil carbon refers to all litter on the ground as well as the humus layer and SOM down to a depth of 1 m in mineral soil. The carbon pools of litter and SOM, the annual changes in these pools and heterotrophic respiration resulting from decomposition were calculated using the dynamic Yasso soil carbon model (Figure 9) (Liski et al. 2005). This model simulates the cycling of carbon in upland forest soils down to a depth of 1 m in mineral soil. The Yasso soil model consists of five decomposition compartments and two woody litter compartments. The dynamics of these compartments are controlled by the physical and chemical quality of litter and climate. The chemical quality of litter is accounted for by dividing the litter among three decomposition compartments having different decomposition rates. One of these compartments is for the most easily decomposable compounds, while the others are for cellulose and lignin; the division is done according to the actual concentrations of these compounds in the litter. The remaining two decomposition compartments are for humus formed in the decomposition process. The physical quality of litter is taken into account by dividing woody litter between the compartments of fine (branches and transportation roots) and coarse woody litter (stem and stump) and releasing it for actual decomposition at a higher rate from the compartment of fine woody litter. The climatic controls of decomposition are temperature and summer drought. In the present study, the effect of summer drought was excluded since temperature alone explains more than 85% of the climatic effects on decomposition on an annual basis in Finland (Liski et al. 2003a).

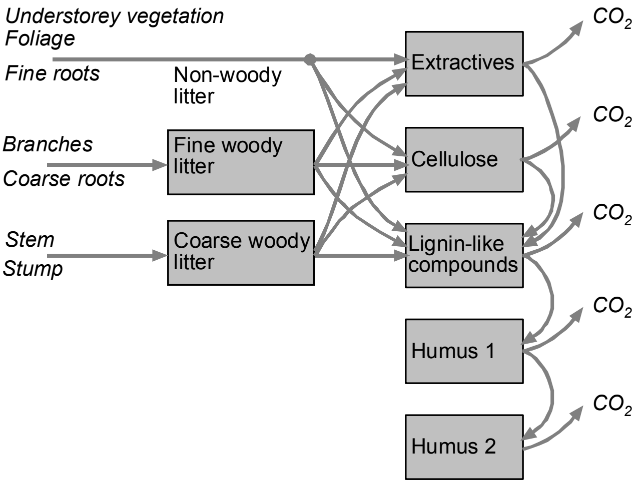

Figure 9. Flow chart of the Yasso model (Liski et al. 2005). The boxes represent carbon compartments, the arrows carbon fluxes.

The Yasso litter and soil model was calibrated using data from forests in Finland and neighbouring countries (Palosuo et al. 2005). However, this model also contains equations that describe the effects of climate on decomposition and therefore it may be used in a wide range of environments (Liski et al. 2005, Palosuo et al. 2005). When compared according to field measurements, the Yasso model provided adequate estimates of the amount of soil carbon (Peltoniemi et al. 2004). In the present study, only mineral soils were examined because the Yasso model was not applicable to peatlands (Liski et al. 2005).

The carbon pools of soil and litter at the beginning of the study period were calculated by assuming the presence of a steady state with mean litter input between 1922 and 1936 and mean temperature between 1901 and 1930 (**V**). Beginning from this steady state in 1922, the model was run using annually varying values of litter input and temperature.

Changes in forest soil carbon are dependent on a balance between the accumulation of dead biomass, its incorporation into the soil and losses due to respiration and decay. The rates of litter input and decomposition can be influenced by management practice, while any change in climate, particularly rainfall patterns and temperature, will also affect the rate of carbon loss or gain in forest soils. Any soil disturbance associated with forest management may release carbon to the atmosphere and should be minimized to optimize soil carbon stock.

3.2 Remote sensing methods

*3.2.1 Spectral feature extraction ASTER data (**VI**)*

The mean reflectances were extracted for each forest stand to explain the variation in aboveground biomass of trees and understorey vegetation, stand volume, and age. Due to the relatively small mean stand size, a large number of pixels were located on the borders of the forest stands. These mixed pixels received responses from two or several stands. To avoid this, we used only those pixels located in the core areas of the forest stands as Kilpeläinen and Tokola (1999), Hyvönen (2002), and Mäkelä and Pekkarinen (2004) have also done. This resulted in a wide area on the border of the forest stand, which was left unused to compensate for the rectification errors in the remote sensing data and forest stand maps. Those forest stands that had no core pixels were excluded from further analysis.

*3.2.2 Statistical modelling of ASTER data (**VI**)*

Nonlinear regression analysis and neural networks were employed in statistical modelling of the relationship between the forest variables and ASTER data. Both regression analysis and neural networks successfully employed in the estimation of forest attributes, using remote sensing data (Ardö 1992, Häme et al. 1997, Hyyppä et al. 2000, Boyd et al. 2002, Foody et al. 2003).

Nonlinear regression analysis using spectral bands $ASTER_{(\mathrm{RED})}$ and $ASTER_{(\mathrm{NIR})}$ as predictors was undertaken to develop models

$$\begin{aligned} y_i &= \exp(\beta_0)\cdot\left(1 + ASTER_{(RED)}\right)^{\beta_1}\cdot\left(ASTER_{(NIR)}\right)^{\beta_2}\cdot\exp\left(\beta_3\cdot ASTER_{(RED)}\right)\\ &\cdot\exp\left(\beta_4\cdot ASTER_{(NIR)}\right)+\varepsilon \end{aligned} \tag{12}$$

for forest attributes (y_i) other than the biomass of understory vegetation (**VI**). The model for the biomass of understory vegetation was

$$y_i = \beta_0 + \beta_1 \cdot ASTER_{(RED)} + \beta_2 \cdot ASTER_{(NIR)} + \varepsilon \,. \qquad (13)$$

In these models, the β_0– β_4 are the parameters and ε the error term.

Several model types and attribute combinations were tested and compared. The combination of red and NIR spectral bands (2 and 3, respectively) seemed to predict the forest attributes more reliably than any other single band or any other simple combination of spectral bands.

Regression analysis can produce inaccurate estimates (Boyd et al. 2002, Foody et al. 2003), but it is also difficult to satisfy the underlying assumptions. Neural networks are general-purpose computing tools that can be used to solve complex nonlinear problems (Bishop 1995). The major attraction of neural networks is that they offer a powerful means for analysing complex datasets without making assumptions about them, as do conventional statistical methods (Boyd et al. 2002).

A range of different network properties was investigated but attention was focused on the network type providing the most reliable predictions of the forest variables. The networks employed had 2 hidden layers with 5 hidden nodes between the input and output neurons, i.e. between the ASTER bands and forest variables. The networks were trained by the Levenberg-Marquardt algorithm (Levenberg 1944, Marquardt 1963).

*3.2.3 Simultaneous use of ASTER and MODIS data (**VII**)*

Published regression models (**VI**) for estimating aboveground biomass (t ha^{-1}) using ASTER satellite data were applied directly to the MODIS data covering the southern Finland (**VII**) (for calculation scheme see Figure 10). The forest mask was constructed using Finnish Corine Land Cover 2000 land-use data (25 m × 25 m) produced by the Finnish Environment Institute (CLC2000-Finland 2005).

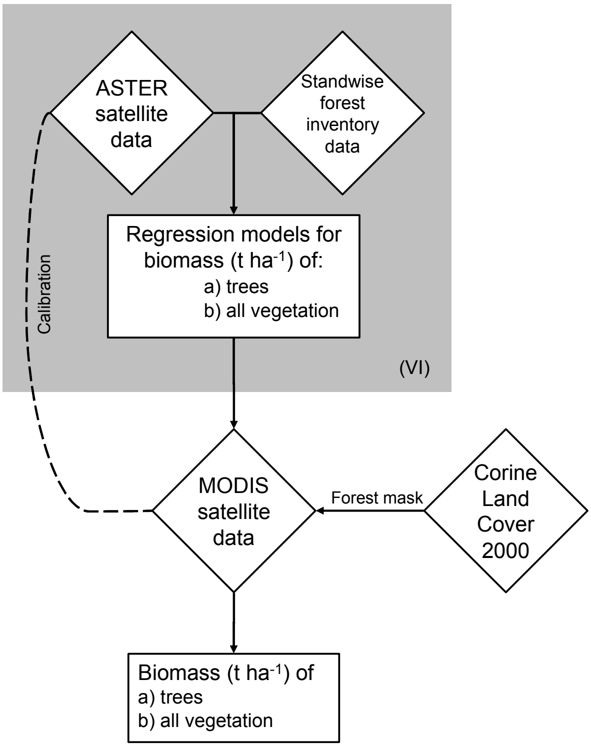

Figure 10. Data-processing scheme during simultaneous use of ASTER and MODIS data (**VII**).

4 RESULTS AND DISCUSSION

4.1 Understorey vegetation (I, II)

The results (**II**) indicate that the aboveground biomass of understorey vegetation can be predicted by such forest site attributes as stand age and site fertility (Figure 11). The importance of age in explaining the variation of biomass in upland forests was also reported in other studies describing successional development (e.g. Lindholm and Vasander 1987, Crowell and Freedman 1994). The understorey vegetation of the Boreal Zone undergoes successional stages after clear-cutting or fire disturbance (Alaback 1982). Just after clear-cutting, the biomass of mosses and field layer plants decreases drastically (Palviainen et al. 2005a, b). The biomass of mosses does not return to pretreatment levels for five years, however, after the initial decrease the field layer biomass increases to levels greater than before clear-cutting. These relatively short-term changes are not, however, detected by the models here, which were constructed to describe long-term changes in understorey biomass (Figure 11).

The predictions here were relatively accurate compared with to previous studies. Mälkönen (1974) reported that in his pine-dominated upland study areas in southern Finland (three 28- to 47-year-old forest stands) the total aboveground biomass of understorey vegetation was 2800–3300 kg ha^{-1}, which is very close to our results (Figure 11). Havas and Kubin (1983) calculated that on their spruce-dominated upland study site in northern Finland the total aboveground biomass of understorey vegetation was 5527 kg ha^{-1}, which lies just slightly beyond the 95% confidence intervals of the models presented here. The difference can be explained by the relatively large amount of dwarf shrubs. Mälkönen (1977) observed in a birch-dominated study site in southern Finland a total aboveground biomass of understorey vegetation of 1100 kg ha^{-1}, which is quite close to the estimate predicted by our models (Figure 11).

The results (**I**, **II**) provide robust and rapid nondestructive tools for estimating the amount of biomass of understorey vegetation under conditions encountered in boreal environments. Yet, the understorey vegetation is a highly diverse component of the forest ecosystem and is not easily predicted with forest site attributes. Many factors, other than those easily observed, affect the biomass of understorey vegetation. Interspecies relationships can drastically impact the occurrence and abundance of a plant species, these influencing the species composition and total biomass of the understorey vegetation.

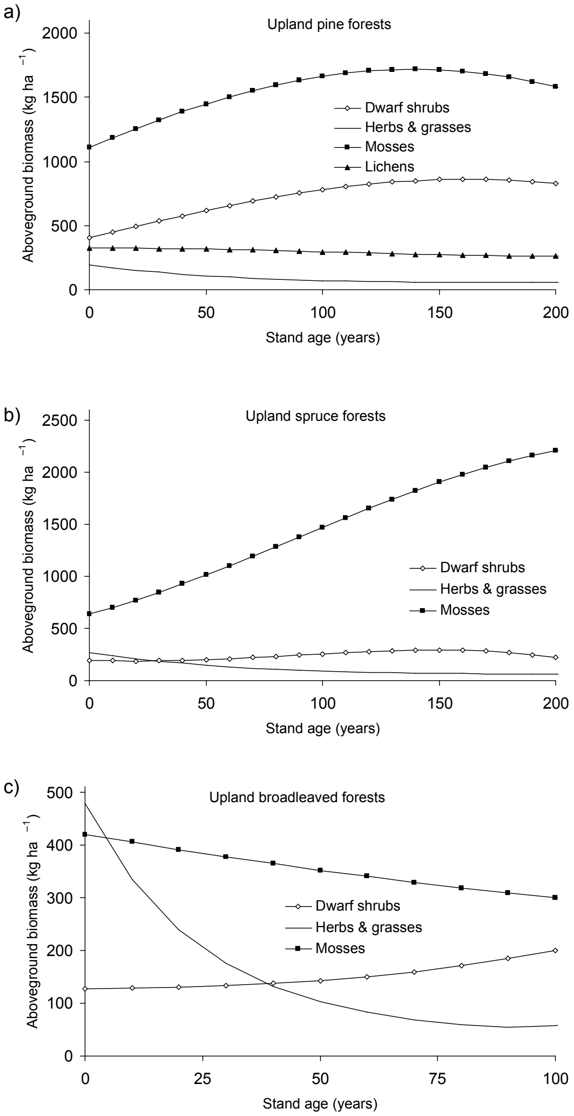

Figure 11. Groupwise aboveground biomass of understorey vegetation in upland forests during stand development. Subfigures a–c represent pine, spruce and broad-leaved forests, respectively (**II**).

4.2 Needle litter (III, IV)

To study needle-shed dynamics and to estimate the turnover rate of needle biomass, ordinal regression was used to model the relationship between age of the needle cohort and the survival class (Figure 12). The results (**III**, **IV**) show that the rates of biomass turnover calculated in this study provide estimates of litterfall that are similar to the measured amounts of litterfall (Figures 13 and 14) and thus can be relevant and useful tools for estimating the average amount of needle litterfall. These biomass turnover rates can provide useful litter production estimates for large areas with average biomass values as a source data. In studies concerning the carbon balance of forests, rates of biomass turnover are usually estimated from few litterfall measurements, or inverse number of the maximum number of needle cohorts is used. When the constant biomass turnover rates were applied (**V**), the NPP estimate from forests in Finland, equal to 0.40 kg m^{-2} y^{-1} in the 1990s, was well within the range of measurements (0.22–0.46 kg m^{-2} y^{-1} at six forest sites in the Nordic countries (Gower et al. 2001).

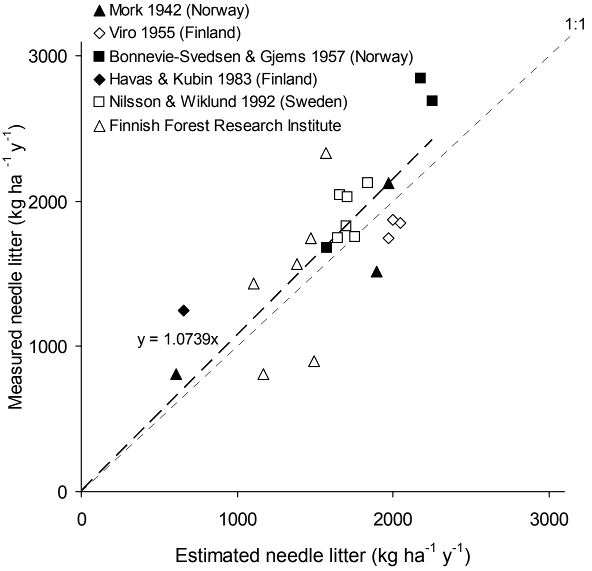

Figure 12. Predicted survival percentages with 95 % confidence limits for Norway spruce needle co-horts in the cohort approach, according to age of the needles (**IV**).

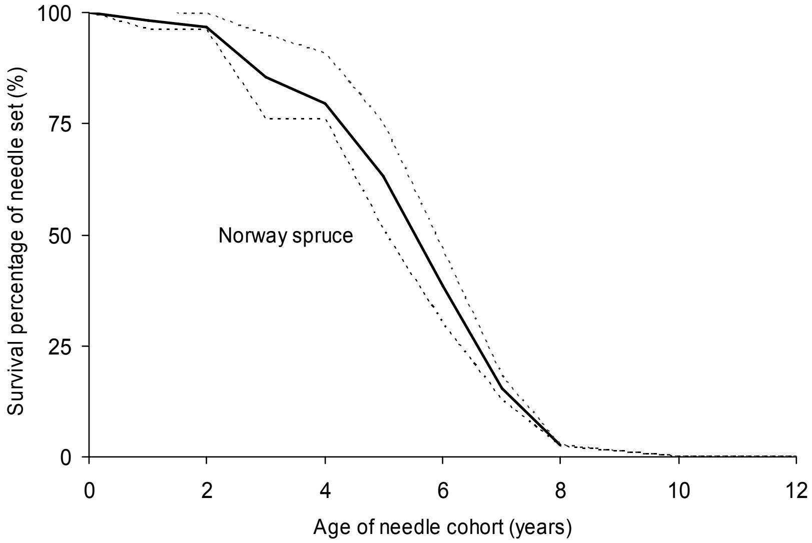

Figure 13. Comparison of modelled and measured needle litterfall of Norway spruce (**IV**). The biomass turnover rate was compared with the results of litter trap studies (Mork 1942, Viro 1955, Bonnevie-Svedsen and Gjems 1957, Havas and Kubin 1983, Nilsson and Wiklund 1992).

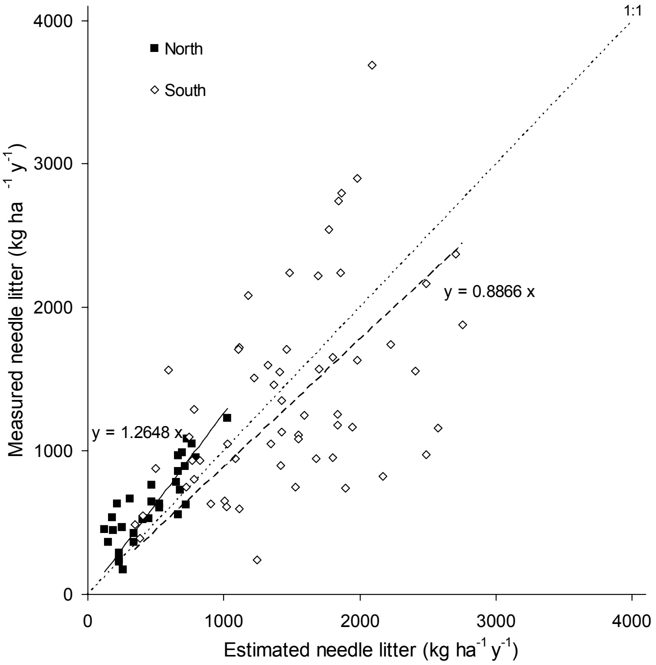

Figure 14. Comparison of modelled and measured needle litterfall in Scots pine forests (**III**). The biomass turnover rate for southern Finland was compared with the results of litter trap studies at the same latitude (Mork 1942, Viro 1955, Bonnevie-Svedsen and Gjems 1957, Mälkönen 1974, Bringmark 1977, Albrektson and Andersson 1978, Flower-Ellis and Olsson 1978, Albrektson 1988, Kouki and Hokkanen 1992, Finér 1996, Krankina 1999, Mälkönen et al. 2000, Starr et al. 2005). The biomass turnover rate for northern Finland was compared with the results of litter trap studies at the same latitude (Falck 1981, Alaback and Herman 1988, Mälkönen et al. 2000, Starr et al. 2005).

4.3 Carbon accumulation in Finland's forests (V)

Carbon has accumulated in the biomass, litter and soil of Finland's forests during the study period (Figures 15 and 16). Similar increasing trends of the forest carbon stocks were observed everywhere across the Temperate and Boreal Zones during recent decades (Goodale et al. 2002, Liski et al. 2003b). The reasons behind these trends are known to differ between regions (Kurz and Apps 1999, Chen et al. 2000, Liski et al. 2003b, Nabuurs et al. 2003). In the present study, carbon accumulated in the forests because the forested area and the mean level of carbon per forested area increased. Both the increase in forested area and the increased carbon density in Finland's forests were the results of forest management that aimed at increasing the yield of sustainable timber harvests by increasing the growing stock of trees.

Half of the additional carbon found in the litter or soil was not, however, taken up and brought there from the atmosphere by forest vegetation during the study period but transferred there from other land uses as the forested area expanded. When this C is ignored, after defining carbon sink as process that removes carbon from the atmosphere, the total carbon sink of these forests is 4.0 Tg y^{-1} in which the contribution of the litter and soil is 17% (Figures 15 and 16). The mean amount of soil carbon in Finland in 1990s estimated in this study was 6.3 kg m^{-2}, which is within the range of earlier measurement-based estimates of 6.2–7.2 kg m^{-2} (Kauppi et al. 1997, Liski and Westman 1997).

In addition to these trends towards increase, the annual changes in the carbon balance of both the biomass and the soil were highly variable (Figures 15 and 16). Such interannual variability was shown to be crucial on a sitescale based on measurements of carbon fluxes (Suni et al. 2003) and on a global scale based on ecosystem modelling (Lucht et al. 2002), inverse modelling (Bousquet et al. 2000) and satellite observations (Myneni et al. 1997). Yet, it has not been possible to account for this variability in earlier large-scale studies based on forest inventories, since it has not been possible to derive the annual estimates from these inventories (Goodale et al. 2002). The main factors affecting the interannual variability in this study were climate conditions and harvesting intensity. Warmer climate conditions promoted increase in biomass and thus the uptake of carbon in the forest vegetation but also the decomposition of SOM and litter (see Figure 17) and therefore the release of carbon from these pools to the atmosphere. Again, harvesting had a decreasing effect on the carbon stock of trees but a temporary increasing effect on the carbon stock of litter and soil, because the harvest residues were an important source of litter and soil carbon (Figure 18). As a result of these contrasting effects, the compounded carbon balance of the biomass, litter and soil was less variable than that of any of these components alone.

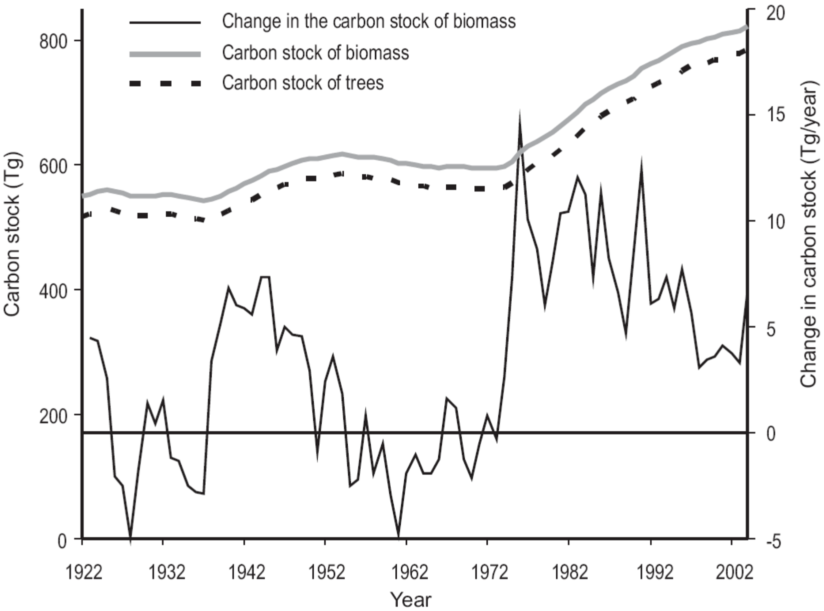

Figure 15. Carbon stock of biomass (trees plus ground vegetation), carbon stock of trees alone and annual changes in the carbon stock of biomass in Finland's forests between 1922 and 2004 (**V**).

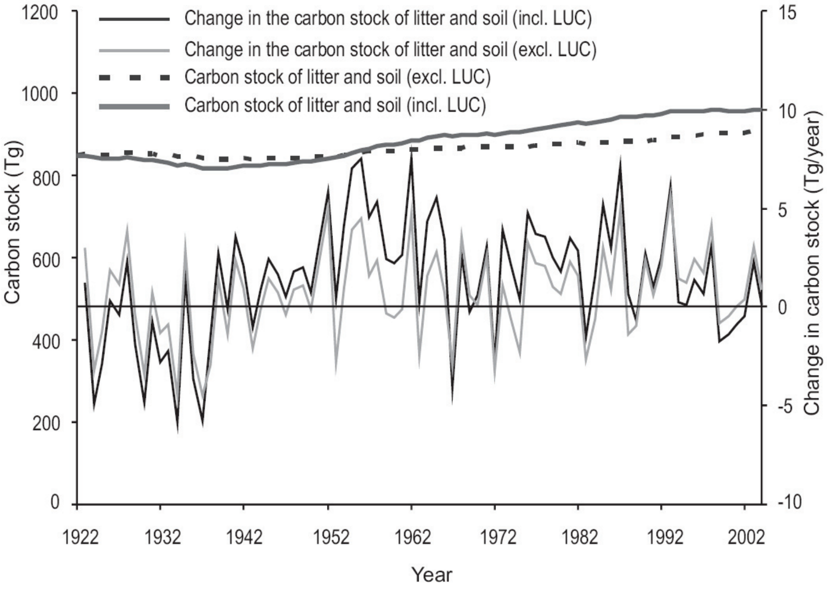

Figure 16. Carbon stock of litter and soil and its annual changes in Finland's forests between 1922 and 2004 (**V**). The black lines show these variables when the transfers of carbon in litter and soil between forests and other land uses were accounted for (incl. LUC) and the grey lines show these variables when these transfers were ignored (excl. LUC).

The accuracy and error propagation of the presented inventory-based large-scale forest carbon budget assessment is studied by Peltoniemi et al. (2006) with Monte Carlo analysis. Uncertainty of the vegetation carbon sink was affected mostly by input data on growth variation and drain. Uncertainty of the soil carbon sink was dominated by the soil model initialization. The most influental parameters for vegetation carbon stock were carbon content and conversion factors for tree and understorey vegetation biomass, and for soil carbon stock, they were soil model parameters, and biomass conversion factors and biomass turnover rates of fine roots and understorey vegetation.

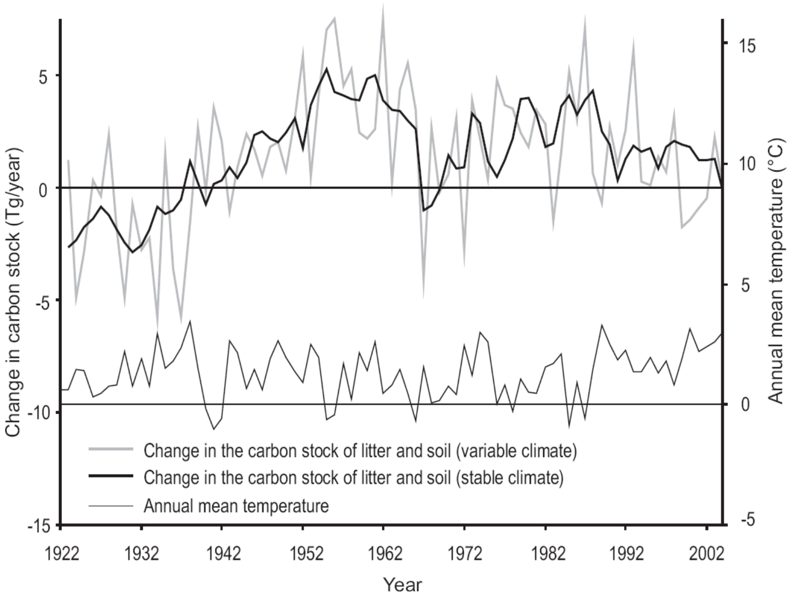

Figure 17. Annual changes in the carbon stock of litter and soil in Finland's forests between 1922 and 2004 when the transfers of carbon in litter and soil between forests and other land uses were accounted for (incl. LUC), simulated using the actual variable climatic conditions or stable average climate. The annual mean temperature of Finland is also shown (**V**).

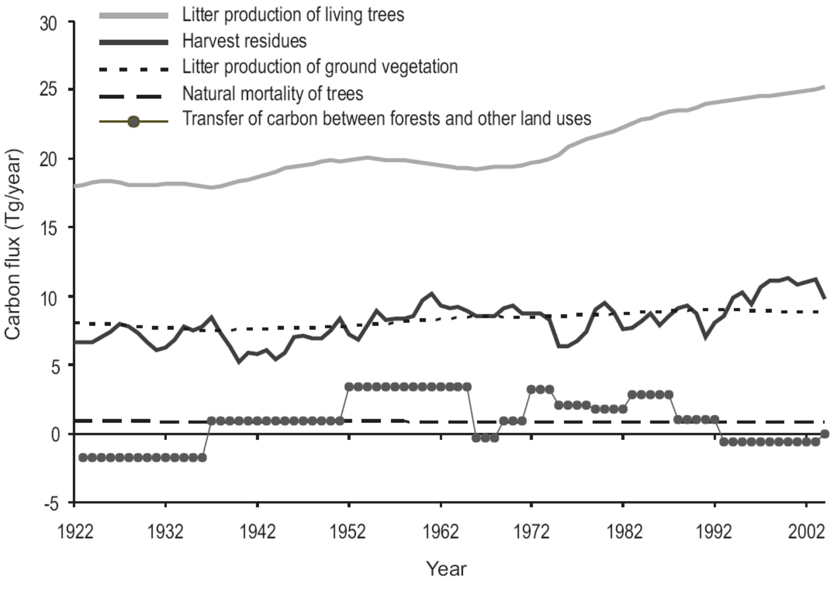

Figure 18. Input of carbon to the carbon stock of litter and soil by origin, and the transfers of carbon in litter and soil between forests and other land uses in Finland's forests between 1922 and 2004 (**V**).

4.4 Comparison with other data sources

*4.4.1 Remote sensing (**VI**, **VII**)*

The optical remote sensing based estimate (**VII**) for the average aboveground biomass of all living vegetation in southern Finland (Figure 19) (85 t ha^{-1}) were quite similar to the forest inventory-based estimate (79 t ha^{-1}) (**V**). In addition, NFI field data are in general only available for small sample plots, while remote sensing methods allow wall-to-wall mapping (full aeral coverage) of forest parameters, especially stem volume, tree biomass and carbon stocks.

The estimation errors reported are high at the pixel level, however, the errors decrease when the sizes of the assessment units increase, e.g. when the pixel-based results are aggregated into larger assessment units. Therefore, we do not recommend that results of article **VII** be used for mapping at the pixel level or for small areas such as forest stands, but instead that they be aggregated into larger assessment units e.g. at the municipality or forestry centre level.

The present results indicate that models for predicting aboveground biomass based on high-resolution (15 m × 15 m) ASTER data (**VI**) can be utilized with coarse-resolution (250 m × 250 m) MODIS data (**VII**). The demonstrated approach can be used as cost-effective tool to produce preliminary biomass estimates for large areas where more accurate national or large scale forest inventories do not exist. The biomass estimation using coarse-resolution remote sensing data has been uncommon because of the big difference between the support of ground reference data and pixel size of the remote sensing data (Lu 2006). In the present study, this problem was managed by using standwise forest inventory data instead of plotwise measurements. The area of forest stands is still too small to integrate standwise forest inventory data directly with coarse-resolution MODIS data. Therefore standwise means of higher resolution ASTER data were used for developing regression models, which were succesfully utilized with MODIS data. The standwise means of higher resolution data correspond to the homogenous pixels of coarse-resolution data and provide the connection between the ground reference data and coarse-resolution sattellite data.

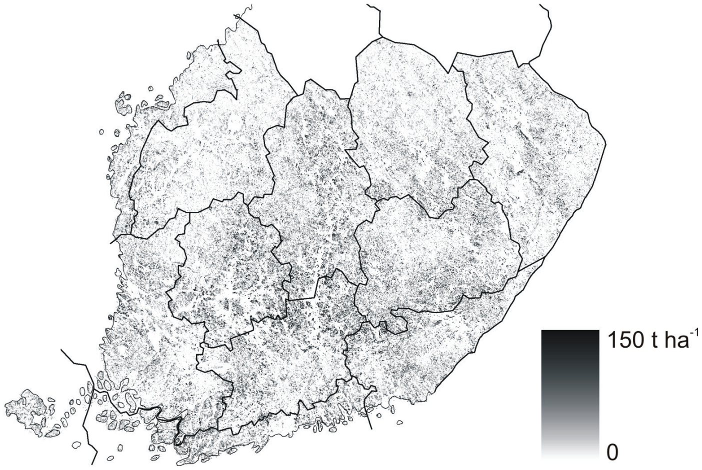

Figure 19. Abovground biomass (t ha^{-1}) of all forest vegetation (trees plus understorey vegetation) based on standwise forest inventory data, ASTER and MODIS satellite data (**VII**).

IPCC GPG (2003) emphasizes that remote sensing techniques can be used as independent methods for comparison of national or regional carbon stock inventories and especially aboveground biomass. Carbon stocks in forests can be estimated using correlations between spectral image data and biomass, provided that adequate data (not used for carbon stock inventory estimates) are available to represent the range in forest biomes and management regimes for which estimates are required (Trotter et al. 1997). The method illustrated in the present study, can therefore be used as required for independent comparisons data since it is based on the use of independent ground reference data, which is the most important requirement for useful comparisons (IPCC 2003).

4.4.2 Measurements of greenhouse gas fluxes

In the 1990s, the estimated NPP of the Finland's forests averaged 0.374 kg carbon m^{-2} y^{-1} (Figure 20). In addition, the estimated average NEP (Net Ecosystem Productivity) in the 1990s was 0.10 kg carbon m^{-2} y^{-1} (Figure 21), which is in the midrange of NEP measurements taken at six forest sites in the Nordic countries, varying from a carbon source equal to –0.09 kg m^{-2} y^{-1} to a carbon sink equal to +0.25 kg m^{-2} y^{-1} (Valentini et al. 2000). On the other hand, the present estimate is lower than measurements taken at a 40-year-old Scots pine stand in southern Finland where they ranged from 0.23 to 0.31 kg m^{-2} y^{-1} between 1997 and 2000 (Suni et al. 2003). This is understandable since our estimates (mean value for whole Finland) contain also low-productive forests in northern Finland.

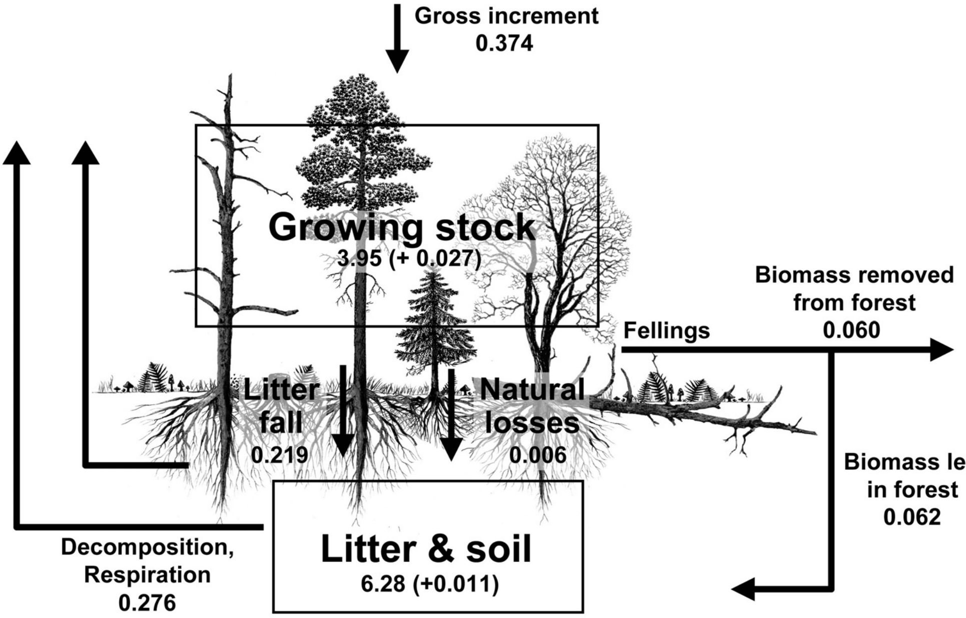

Figure 20. Average carbon budget of Finland's forests in the 1990s (carbon stocks kg m^{-2}, carbon fluxes kg m^{-2} y^{-1}) (**V**). (Gross increment = Photosynthesis – Autotrophic respiration; compare to Figure 1).

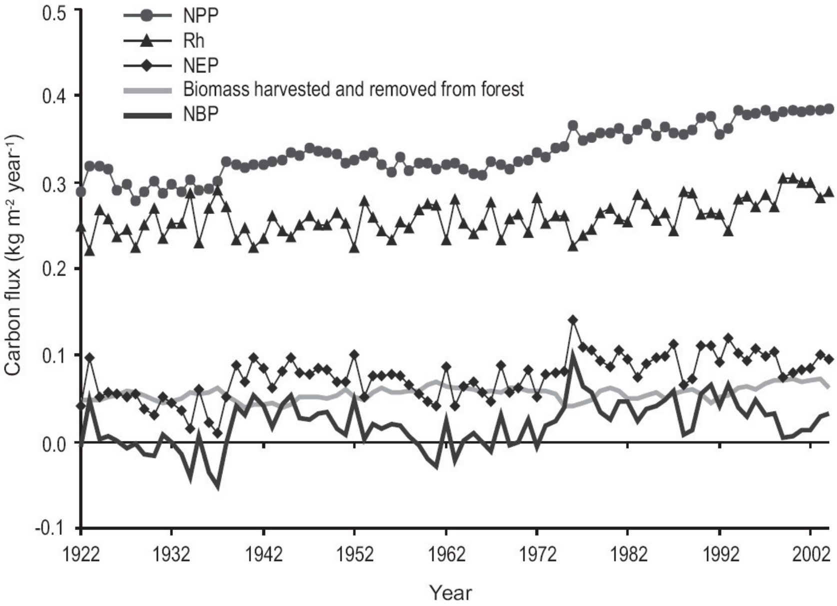

Figure 21. Carbon fluxes in Finland's forests between 1922 and 2004 (**V**). NPP = net primary productivity, Rh = heterotrophic respiration, NEP = net ecosystems productivity, NBP = net biome productivity.

5 CONCLUSIONS

A variety of methods can be used to estimate the level of variation in carbon stocks of different pools in forest ecosystems. All of these methods have advantages and disadvantages; the usefulness of the results is strongly dependent on the objectives, data source and geographical scale. In general, it is possible to obtain detailed information on greenhouse gas balances at a local level. The great challenge, however, is to develop and apply methods that result in estimates on the large scale, with acceptable accuracy, in a cost-efficient way.

The present study demonstrates that it is possible to calculate appropriate estimates for the complete carbon balance of forests based on general forest inventory data, by complementing these data with modelling (**V**). The estimations and methods provided in the present study were developed principally for large-scale assessments of forest carbon resources. The overall precision of these carbon estimates varies, depending on the application. For example, applying these methods to a specific forest stand would not provide a precise estimate of the carbon stock for that site but rather an estimate of the large-scale average for similar sites. The method described here represents a robust and cost-effective way of monitoring nationwide carbon stocks and stock variations. The method developed here can be applied throughout the Temperate and Boreal Zones to calculate comparable estimates for carbon balance of the forests.

The carbon budgets of trees and forest soil have been modelled extensively, but understorey vegetation is not usually included in these analyses and appropriate methods for estimating its biomass, which are applicable in large-scale studies, are not available. However, the biomass of understorey vegetation may play an important role in many ecosystem processes, e.g. in the nutrient and carbon cycles. Robust tools are provided (**I**, **II**) for estimating the aboveground biomass of understorey vegetation under conditions encountered in boreal environments. Firstly, models can be used for rapid nondestructive determination of the aboveground biomass when direct biomass measurements are not available but the percentage cover of different plant species is or can be recorded (**I**). Secondly, the modelled relationship between the biomass of understorey vegetation and forest site attributes can be used in forest carbon balance modelling as a rapid nondestructive method for predicting the aboveground biomass of understorey vegetation (**II**).

To understand the carbon cycle and flows of forests, reliable information on tree component-specific litter production is needed. The biomass turnover rates developed enhanced forest inventory-based large-scale carbon stock assessment, and give adequate estimates of mean litterfall (**III**, **IV**).

The remote sensing method illustrated (**VI**, **VII)** can be used as required for independent comparisons; the remote sensing method tested 1) provides adequate large-scale average biomass estimates and 2) is based on the use of independent ground reference data, which is the most important requirement of useful comparisons.

The NFIs provide statistically sound and in most cases reliable information on forest resources throughout the Temperate and Boreal Zones. Since the reliability of forest inventory data on forest area, growing stock and growth of timber is good, the reliability of the estimates for carbon balance is dependent mainly on the other components of the calculation scheme presented in Figure 6. Understanding the interacting processes and the quantitative relationship between different carbon pools in boreal forest ecosystems and site characteristics, and climatic conditions on a finer scale is the key to improving projections of forest carbon budgets and their variations. To improve large-scale forest carbon stock assessment, information on the biomass estimates of understorey vegetation was based only on stand age and main tree species. Yet, there are many other factors affecting forest carbon stock and these must be quantified. Information on the biomass of the belowground parts of both trees and understorey vegetation is also needed. In addition, further knowledge on understorey vegetation litter production is required as well as on the biomass turnover rates of roots and different components of broad-leaved trees. Since the present study deals only with upland mineral soils, this methodology should also be expanded to cover peatlands.

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ERRATUM

In the article **I**, the following correction should be made:
In the figure 2, labels of x- and y-axes have reversed their positions.

This correction is only typographical in nature, and none of the results or conclusions of the paper are affected.