Dissertationes Forestales 88

From a tree to a stand in Finnish boreal forests: biomass estimation and comparison of methods

Chunjiang Liu

Department of Forest Ecology
Faculty of Agriculture and Forestry
University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Room B4, Latokartanonkaari 7, Viikki, Helsinki, on May 8th, 2009, at 12 o'clock noon.

Title of dissertation: From a tree to a stand in Finnish boreal forests: biomass estimation and comparison of methods

Author: Chunjiang Liu

Dissertationes Forestales 88

Thesis Supervisors:
Prof. Carl Johan Westman
Department of Forest Ecology, University of Helsinki, Finland

Pre-examiners:
Docent Heljä-Sisko Helmisaari
The Finnish Forest Research Institute, Vantaa, Finland

Prof. Arne Albrektson
Swedish University of Agricultural Sciences, Umeå, Sweden

Opponent:
Prof. Leena Finér
The Finnish Forest Research Institute, Joensuu Research Unit, Joensuu, Finland

ISSN 1795-7389
ISBN ISBN 978-951-651-265-8 (PDF)

(2009)

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

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

Liu, C. 2009. From a tree to a stand in Finnish boreal forests: biomass estimation and comparison of methods. Dissertationes Forestales 88. 43 p.
Available at http://www.metla.fi/dissertationes/df88.htm

ABSTRACT

There is an increasing need to compare the results obtained with different methods of estimation of tree biomass in order to reduce the uncertainty in the assessment of forest biomass carbon. In this study, tree biomass was investigated in a young 30-year-old Scots pine (*Pinus sylvestris*) and a mature 130-year-old mixed Norway spruce (*Picea abies*)-Scots pine stand located in southern Finland (61°50' N, 24°22' E). In particular, a comparison of the results of different estimation methods was conducted to assess the reliability and suitability of their applications.

For the trees in the studied mature stand, the annual stem biomass increment increased following a sigmoid equation. The fitted curves reached the maximum level (from about 1 kg yr^{-1} for understorey to 7 kg yr^{-1} for dominant tree) in the studied stand when the trees were 100 years old.

The results revealed a substantial difference in tree stand biomass among estimations made by different methods. For instance, at stand level, on the basis of the above-ground tree biomass (170.8 Mg ha^{-1}) estimated by partial harvesting method, it had a higher estimate (+10%) based on the dry mass of selected understorey, medium and dominant trees as the sample trees, but a lower estimate (–18%) by the means of the allometric functions which were established based on the tree data in Sweden.

In the studied mature stand, lichen biomass on the trees was estimated at 1.63 Mg ha^{-1} with more than half of the biomass being on dead branches, and litter lichen biomass on the ground was about 0.09 Mg ha^{-1}.

Based on a data set compiled from the studies previously published, a meta-analysis was conducted to compare the tree biomass accumulation in southern Finland with that in the boreal region (58.00-62.13 ºN, 14-34 ºE, ≤ 300 m a.s.l.). The results showed that in this region the average total tree biomass was about 180 Mg ha^{-1} with the range of 100 to 250 Mg ha^{-1} at the age of 140 years in Norway spruce and Scots pine stands. The total tree biomass of two stands in the present study was at the average level at corresponding stages of age in this region.

Key words: Tree biomass, boreal forests, estimate methods, lichen

ACKNOWLEDGEMENT

I was introduced to touch with the topic, forest biomass and productivity, as a young researcher in the beginning of the 1980s when I worked as a master student together with Prof. Guofang Shen at Beijing Forestry University, China. In my master's thesis the estimation of net primary productivity and biomass in both pure and mixed stands of *Pinus tabulaeformis* and *Quercus variabilis*, two dominant tree species in natural forests in temperate China, was dealt with. The two papers based on the data of my master's thesis were ones of earliest publications concerning forest biomass in Chinese literature. Since then this topic has been one of my research interests.

At that time, forest biomass investigation was a very hot topic due to its incipient period in China. Since then more than 20 years went by, our generation is not young, but this topic is seemingly still hot. In particular, forest biomass, a scientific term in the field of forest science, has been more and more discussed not only by forest ecologists, but also by scientists in other fields, government officers, businessmen, and public. Such a social phenomenon occurs mainly because the functions of forest ecosystems, other than raw materials, are widespread realized regarding to human future. Especially the forest biomass worldwide is a huge storage of carbon, and forestry management was accepted a strategy for mitigating atmospheric CO_2 increase with implement of the Kyoto Protocol. In this context, it becomes an important issue to estimate accurately the biomass from a tree, to a stand and to global forests.

It is really a simple task to weigh a piece of wood, but indeed a complicated matter to estimate the biomass for a tree or in a stand. While collecting data and writing the individual papers and summary of the dissertation, I really experienced the complexity, difficulty and bemusement in doing such a 'simple' task. Meanwhile I was also enjoying a lot of happiness when I got some simpler patterns from such complicated phenomena.

With finishing this dissertation, firstly my thanks go to Prof. Carl Johan Westman, supervisor of my dissertation, for his help, encouragement, and friendship. Indeed, I could not finish this work without his encouragement. I want to thank warmly Prof. Hannu Ilvesniemi, Finnish Forest Research Institute, for his help in my study, assistant in the field work and discussions about research topic during the period of my dissertation work. I wish to thank Dr. Mike Starr for our good collaboration in research and teaching for these years. I am grateful to Prof. Juhani Päivänen and his wife for their solicitudes for my study and my family. Many discussions with Dr. Jukka Pumpunen greatly optimized the contents and format of the dissertation. Prof. Harri Vasander, Drs. Raja Laiho, Eeva-Stiina Tuittila, Jaana Bäck, Jukka Lippu and other colleagues in the Department of Forest Ecology are greatly appreciated for their kind help for these years.

For these years I have had a fruitful collaboration with Prof. Björn Berg, Dipartimento Biologia Strutturale e Funzionale. Complesso Universi-tario, Italy, which greatly benefits to completing my dissertation. I am grateful to Prof. Pekka Kauppi, Dept. of Environmental Science and Policy, University of Helsinki, for the intriguing discussions about forest biomass and global carbon cycling. I greatly appreciate Dr. Ilkka Linnankoski, Institute of Biomedicine, University of Helsinki, for language checking on this dissertation and his family's friendship with mine. My warmest thanks also go to Prof. Antti Pertovaara and Prof. Synnöve Carlson, Institute of Biomedicine, University of Helsinki, for their concern about my work and my family.

At this moment, I would also like to acknowledge my Finnish friends, Soili Poikonen and Jari Hyle, and their children for their hospitality, friendship, and tasteful Finnish family food, and my Chinese friends who are now here and somewhere else in the world, Shunxing Chen, Yucheng Dai, Zhihe Gao, Deyin Guo, Zhangren Lan, Chunmei Li, Chunyang Li, Guifang Lu, Jinrong Lu, Xiu Sun, Fan Yang, Guang Yang, Yaoqi Zhang, Chunmei Zhang, Xiaolu Zhang, Xuejiao Zhou and others for their sincere concern and lasting friendship.

This work was financially supported in part by The Finnish Society of Forest Science and Finnish Graduate School of Forest Sciences. Field investigations were conducted in Hyytiälä Forestry Field Station where I spent two summers with a good impression of beautiful landscape, well-equipped laboratory facilities and full support to my work.

Finally, and most importantly, I would like to thank my wife, Hong Wei, our son, Xinxin and our daughter, Lili for their love, understanding and support. For these years, my wife has continuously supported me and taken care of our children, and they always bring me so much happiness and enjoyment which are the driving force for my work, in particular, when I meet with difficulties. I always remember the love and concerns from my late father and mother, my sisters and brother and their full support to my study and work. For these years, my late father-in-law, my mother-in-low, and my sisters- and brother-in-law have all shown great interests to my dissertation work and offered a hearty support, being an encouragement and spur on my work. Here, I would like to express my heartfelt gratitude and thanks to all you.

Helsinki, May 2009

Chunjiang Liu

LIST OF ORINGAL ARTICLES

This thesis is based on the following articles, which are referred to in the text by their Roman numerals. The articles are reprinted with kind permission of the publishers.

I Liu C., Ilvesniemi H. & Westman C. J. 2000. Biomass of arboreal lichens and its vertical distribution in the boreal coniferous forests in central Finland. The Lichenologists 32: 495-504.

II Ilvesniemi H. & Liu C. 2001. Biomass distribution in a young Scots pine stand. Boreal Environment Research 6: 3-8.

III Liu C., Westman C. J. & Ilvesniemi H. 2009. Annual stem biomass increment related to variation in tree ring-width in boreal Norway spruce and Scots pine (submitted)

IV Liu C. & Westman C. J. 2009. Biomass in a Norway spruce - Scots pine forest: A comparison of estimation methods. Boreal Environment Research (in press).

AUTHOR'S CONTRIBUTION

Chunjiang Liu is responsible for the summary of this thesis. He participated in planning the experiments, collection of the samples in the field, measurements in the laboratory and processing data, which are the basis for Papers I, II, III and IV. Chunjiang Liu was the main author for Papers I, II, III and jointly wrote Paper IV. Carl Johan Westman was responsible for experiment planning, assisted in the field work, and participated in writing Paper I, III and IV. Hannu Ilvesniemi participated in the experiment planning, data collection and writing Papers I, III, and was responsible for writing paper II.

TABLE OF CONTENTS

ACRONYMS AND ABBREVIATIONS

Symbol	Description
ABH	Stem cross-sectional area at breast height, cm^2
AGB	Above-ground biomass, Mg ha^{-1}
Altit	Altitude, m
ANPP	Above-ground net primary productivity, g m^{-2} yr^{-1}
APP	Annual precipitation, mm
AP	Average dominant pine
BEFs	Biomass expansion factors
BGB	Below-ground biomass, Mg ha^{-1}
C	Carbon
DBH	Diameter at breast height, cm
DS	Dominant spruce
FAO	Food and Agriculture Organization
HPDB	Height position of first dead branch, m
HPLB	Height position of first living branch, m
IBP	International Biological Program
Latit	Latitude, º
Longit	Longitude, º
MAT	Mean annual temperature, ºC
Mature-Stand	130-year-old Norway spruce and Scots pine stand
MS	Medium spruce
NLB	Number of living branches
NPP	Net primary productivity, g m^{-2} yr^{-1}
SS	Understorey spruce
SW	Specific weight of stem wood, kg m^{-3}
TBNA	Total basal neck area of living branches
TTB	Total tree biomass, Mg ha^{-1}
Young-Stand	30-year-old Scots pine stand

1 INTRODUCTION

1.1 Estimation of forest biomass

According to Satoo (1982), the earliest measurement of tree biomass was made by the German scientist Ebermeyer E. in 1876. He measured only the amount of leaves and branches in forests. During the first half of the 20th century, thorough investigations of the various components of forest biomass (foliage, branches, stem, and roots) were started in some countries, e.g. Germany, Switzerland, Japan (see Satoo 1982). These early studies aimed mainly at the utilization of biomass as a forest resource. In the 1960s, with the implementation of International Biological Program (IBP), forest biomass and net primary productivity (NPP) were, for the first time, systematically studied worldwide (except e.g. in China), resulting in accumulation of biomass data and the development of new methods to estimate biomass (DeAngelis *et al*. 1981, Satoo 1982, Madgwick 1982, Cannell 1982). At that time, in the shadow of the oil crisis of the early 1960s, the importance of biomass energy was realized, and scientists started to point out how much dry matter was stored in forest ecosystems and how biomass and NPP were controlled by various environmental factors at the stand, regional and global scales (Lieth 1975, Waring & Franklin 1979). In the early 1980s, Chinese scientists started a nationwide investigation on forest biomass and productivity in China, and since then large quantities of forest biomass data have been published (see Feng *et al*. 1999, Fang & Wang 2001). Since the 1980s, the quantity of forest biomass, the factors influencing it and the estimation methods regained their significance on a global scale due to carbon storage and its potential in mitigating atmospheric CO_2 (Brown et al. 1989, Kauppi *et al*. 1992, Brown 1997, Brown et al. 1999).

Generally, forest biomass in a stand is defined as the amount of dry matter or carbon contained in woody plants (trees and shrubs), grasses, ferns and bryophytes per unit area (g m^{-2}, Mg ha^{-1}). In a forest stand, tree biomass is usually the major fraction of standing biomass. Tree biomass is frequently divided into different components according to physiological functions, e.g. foliage, branches, stem, stump and roots. In this study, the main emphasis is on the estimation of biomass at tree and stand scales.

Traditionally, stand biomass estimates are based on harvesting and measuring the dry mass of sample trees (Zhai 1982, Rana et al. 1988, Parresol 1999) and use of allometric functions (e.g. Whittaker & Woodwell 1968, Satoo 1982, Muukkonen 2007, Pajtíka et al. 2008). Allometric functions established in one area are often expected to be applicable to reas with a similar climate and other conditions, e.g. site conditions, silvicultural measures (Kärkkäinen 2005). The forest biomass data obtained by different methods at site level are cited when large-scale (e.g. national and global) forest biomass is estimated (e.g. Feng et al. 1999, Gower et al. 2001). In this context, it is essential to compare and assess the methods that have previously been used in biomass investigations; so that the uncertainties in estimating the carbon stored in forest biomass can be reduced. As early as the 1960s, when many biomass investigations started, the necessity of comparing results obtained by different methods was indicated on the basis of field investigations (Ovington et al. 1967). Since then, however, only a few such field-based comparisons have been carried out, perhaps because they require heavy and destructive field work.

Recently, new approaches and methodologies have been developed to estimate forest biomass, e.g. inventory data (Fang et al. 1998, Fang & Wang 2001, Fournier et al. 2003, Somogyi et al. 2007), radar (Rignot et al. 1994, Næset 2002), and the remote sensing technique (Luther et al. 2002, Drake et al. 2003, Tackenberg 2007, Zheng et al. 2007). However, many uncertainties in forest biomass estimation based on these new approaches remain. Thus there is a need for validating biomass estimates obtained with these approaches using the data compiled by conventional methods as a base line (Houghton et al. 2001, Hiura 2005).

1.2 Annual stem biomass increment

Forest biomass is in a dynamic process in a stand with annual increase (net primary production, NPP) and loss (e.g. herbivores) in dry matter (IGBP 1998). Generally a larger fraction of NPP is allocated to tree stem biomass in a stand, e.g. *c.* 25-38% of NPP in 28-47 years old Scots pine stands in southern Finland (Mälkonen 1974). In this sense, it is essential to investigate the pattern of variation in annual stem biomass increment in individual trees during the period of growth for understanding the dynamic of tree biomass at the stand level.

With regard to calculating the annual stem biomass increment in a tree, two factors need to be taken into account: width of tree ring and wood density. The width of a tree ring formed in one year varies along the stem of a tree, while the width of consecutive rings at a given stem position fluctuate in radial direction (e.g. Brookhouse & Brack 2008). Such stem-vertical and radial variations in ring width are due either to the allometric nature of tree growth (Niklas 1994) or the effects of variation in environmental factors (Fritts 1976, Cook and Kairiukstis 1989, Eronen and Zetterberg 1996, Schweingruber 1996), in particular, climate (e.g. Jacoby et al. 1996, Barber *et al*. 2000). The wood density of a stem for a tree species varies geographically across its distribution area due to differences in climatic factors, site conditions, the origin of stand and silvicultural measures (Baker et al. 2004). At a specific site, the wood density of a stem is affected by the position of the tree in the stand, tree age and size, growth rate and genetic factors (Hakkila 1979). The wood density of a tree also varies in the radial and vertical directions of the stem according to a species-specific pattern (Hakkila 1979, Repola 2006). For instance, the wood density of Scots pine, Norway spruce and birch (*Betula pendula*) stems decreases from the butt to the top, but the gradient of variation in wood density varied among the tree species (Repola 2006).

The annual volume increment of stems can be calculated by means of stem analysis based on ring width measurements (Husch et al. 1982) and the annual biomass increment can be established by including measurements of dry density of stem wood. For a tree, the patterns of inter-annual variation in stem mass increment can be illustrated by calculating the dry mass produced each year. The total stem mass of a tree can be obtained by summing annual increments. Thus, stem analysis provides a method to study the pattern of variation in the annual stem biomass increment and to estimate stem biomass (Bouriaud et al. 2005).

1.3 Biomass of individual trees

Several approaches have been applied to determine the dry mass of branches and foliage of trees. The most accurate method is to separate all the leaves from all the branches and directly determine the dry mass of both components. However, this method is laborious and is rarely used. An alternative method is to select several representative branches from a tree and measure the dry mass of the branches and foliage. Based on the total number of branches and the dry mass of the two components of the representative branches, the corresponding dry mass of the components of the whole tree can be obtained by up scaling (Satoo 1982). This method has been widely applied in the earlier studies (Cummings 1941, Attiwill 1962, 1966), including Chinese and Indian studies (Zhai 1982, Bhartari 1986, Liu 1987, Rawat and Singh 1988). Since the stem of a sample tree is usually divided into sections for stem analysis, one improved way is to select the representative branches and to measure the dry mass by stem section, and then obtain the biomass of the two components by the summing of their dry mass by sections. A more popular method is to systematically collect sample branches from a sample tree, and establish the regression models to describe the relationship between branch cross-sectional area and branch (or foliage) mass (Satoo 1982).

To obtain the root mass of a tree, a direct way would be to dig out all roots of the tree in question. Because of the time consuming and extensive work involved, data on tree root biomass are lacking in published data of forest biomass estimation compared to the amount of data available on above-ground biomass (Cannell 1982, Gower et al. 2001). As a result, more uncertainties exist for root than for above-ground biomass estimations.

The easiest way to estimate the stem biomass of individual trees is to cut the stem into sections and simply weigh them. This is usually done, along with stem analysis, to obtain more detailed information about stem biomass accumulation (Husch et al. 1982, Bouriaud et al. 2005). For species whose allometric functions of biomass have already been obtained, the dry mass of various components (branches, foliage, roots, stem) can be estimated in similar sites with these available functions. During the last few decades, many biomass functions have been established for European boreal tree species (see Zianis et al. 2005, Muukkonen & Mäkipää 2006). However, uncertainties should be taken into account when such functions are employed.

1.4 Tree stand biomass

Forest biomass is the dry mass per unit area of the above- and below-ground parts of live trees and other plants, e.g. shrubs, grasses, mosses, epiphytes in a stand (Cannell 1982, Parresol 1999). Usually tree biomass accounts for most of the total plant biomass in a stand, varying with tree species, age of the trees, site conditions, and management measures. In this study, tree stand biomass is referred to the biomass of all trees in a stand for the sake of convenience.

The most reliable method determining tree stand biomass is harvesting and weighing all trees in a sample plot. A clear-cutting harvest is, however, a destructive, laborious and expensive measure. Thus, tree stand biomass data are usually estimates based on data of sample trees and on the application of regression models using diameter at breast height (DBH) solely or together with height (H) (Crow 1971, DeAngelis et al. 1981, Satoo 1982, Cannell 1982, Parresol 1999).

The diameter and height, crown of trees in a stand varies even for even-aged and pure stand because of competition among trees, genetic differences, and the damage resulting from disease and pests. Trees in a stand are frequently categorized into dominant, co-dominant and understory trees according to their growth status (Bohn & Nyland 2003). For a tree, DBH, height, crown width, stem height under the crown, volume and biomass are important parameters describing the growth status. Thus, it is important to measure the mass of the components of individual trees in the different growth classes for the estimation of the tree biomass in a stand and for the understanding of the allometric relation among biomass components.

The average tree method is also used to estimate the tree biomass in a stand with the assumption that one tree in a growth class (or in a stand) could be selected to approximate the average of total and component dry weight of all trees (Ovington et al. 1967). In this approach, the tree biomass in a stand is simply calculated by multiplying the dry mass of the different components of the average tree in a class by the number of trees in the class and by summing over the stand (e.g. Ovington et al. 1967, Zhai 1982, Rana et al. 1988).

A great number of biomass and stem functions have been obtained for the main tree species in Europe (Zianis 2005, Muukkonen & Mäkipää 2006). Some of the functions have the potential of being applied to a broader area than that where they were established. This type of application would save time and labour, but there would be the problem of uncertainty in the estimates due to a variation in the population properties. Marklund's (1988) functions, which were applied in boreal European forests, are a typical example of this approach. These functions (Marklund 1988) were developed based on a comprehensive data set consisting of 493 Scots pine and 551 Norway spruce trees collected in the forests over Sweden. In the allometric functions of Marklund (1988), DBH solely or together with H are used as independent variables, providing possibility of selecting suitable functions based on users' requirement. These allometric functions (Marklund 1988) have been used to estimate biomass in Norway (Hoen & Solberg 1994) and Finland (e.g. Liski & Westman 1995, Lehtonen et al. 2004) with the assumption that both Finland and Norway have a similar boreal climate with Sweden.

Based on the data of sample trees collected throughout Finland, Kärkkäinen (2005) concluded that Marklund's (1988) functions performed better than those by Hakkila (1979), Issakainen (1988), Finér (1989), Hakkila (1991), Korhonen & Maltamo (1990) and Laiho (1997). This is because the allometric functions of Marklund (1989) were established on the basis of sample trees collected throughout Sweden while the functions of the other studies cited above were based on local sample tree data.

In comparison to above-ground biomass, the estimation of below-ground biomass is more complicated and laborious. Consequently fewer case studies have been conducted to investigate tree root biomass on stand level, and more uncertainties exist in below-ground biomass estimation on large-scale (Cannell 1982, Gower et al. 2001). Usually, in order to measure the below-ground biomass of trees, the stumps and all roots of the sample trees have to be excavated and weighed by size class. The data of these sample trees are then used to estimate at the stand (e.g. Zhai 1982, Bhartari 1986, Liu 1987). Based on the data of sample trees, regression equations between the root mass and DBH are used to estimate the dry mass of different root size fractions in the stands (Satoo 1982, Bao et al. 1984). The dry weight of fine roots (< 2 or < 5 mm in diameter, depending on the definition) can be estimated systematically by core sampling and by determining the biomass of all roots in a given soil layer (e.g. Zhai 1982, Persson 1983, Liu et al. 1985, Pietikäinen et al. 1999 , Helmisaari et al. 2007).

1.5 Biomass of epiphytic lichens and ground vegetation

In boreal forests, both epiphytic lichens and ground vegetation form minor fractions of the total biomass, but they play important functions in such ecosystems (Muukkonen et al. 2006). For instance, epiphytic lichens are important as a winter food source for reindeer and caribou (Andreev 1954, Ahti 1959, Edwards *et al*. 1960, Scotter 1963, Scotter 1964) and as food and shelter for some small animals (Ahti 1977, Gerson & Seaward 1977). Epiphytic lichens also influence nutrient cycling (Knops et al. 1991, 1996) as they absorb nutrients from the substrata and intercept dry and wet deposits from the air. They also modify the quantity and quality of throughfall and stem flow. Investigations of lichen biomass not only focused on the total amount but also on the relative proportion of lichens in a stand and the vertical distribution along the crowns of trees.

In Finnish boreal forests, the ground vegetation layer consists of shrubs, such as *Vaccinium vitis-idaea*, *V. myrtillus* and *Calluna vulgaris*, grasses and sedges, e.g. *Carex* spp., and mosses, such as *Sphagnum* spp., *Dicranum* spp. and *Pleurozium* spp. Mosses frequently form a thick mat-like layer mixed with fresh litter and semi-decomposed litter. This is naturally being used as shelter by small animals. This loose structured organic layer also impacts on the cycling of water and nutrients in the ecosystems due to its water storage capacity and effect on litter decomposition. In this study, however, the biomass of ground vegetation was not addressed due to our focus on tree biomass.

1.6 Biomass estimate in Finnish forests

Finland is located in the western part of the European boreal zone. The forests are dominated by Norway spruce and Scots pine. Due to long-term human disturbance, there are no longer untouched and pristine forests left except in some protected areas in Lapland and Eastern Finland (Kouki *et al*. 2001, Lilja & Kuuluvainen 2005, Rouvinen *et al*. 2005, Huuskonen *et al*. 2008). Plantations, semi-natural or natural secondary forests at varied stages of age dominate in southern Finland (Finnish Statistical Yearbook of Forestry 2007).

During the last decades a lot of work has been done regarding forest biomass measurement and estimation at the stand level in Finnish forests. As early as the 1970's, Mälkonen (1974) determined the annual primary productivity and tree biomass of Scots pine stands in southern Finland. Havas & Kubin (1983) investigated the organic matter content in the vegetation cover of an old spruce forest in Northern Finland, and included epiphytic lichen biomass components. Finér (1989) showed the differences in biomass, biomass increment and nutrient cycling between fertilized and unfertilized stands of Scots pine, Norway spruce and mixed birch (*Betula pubescens*)/ pine on a drained mire in eastern Finland. Laiho & Laine (1997) investigated the tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. Helmisaari (2002) studied the below- and above-ground biomass and production in three Scots pine stands at sapling, pole and mature status in eastern Finland. Lehtonen's (2005) investigated the foliage biomass in Scots pine and Norway spruce stands. Of the above studies, three dealt with stands growing on mineral soil sites (Mälkonen 1974, Havas & Kubin 1983, Helmisaari 2002) and two with peatland stands (Finér 1989, Laiho & Laine 1997).

In addition to site level investigations, a great effort has been made to get more generalized models for forest biomass estimation in Finland. For instance, Hakkila (1979) conducted a systematic study on wood density surveys and dry weight tables for pine, spruce and birch stems. Lehtonen et al. (2004) analyzed biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. On the basis of a survey of literature, Zianis et al. (2005) summarized biomass equations for the tree species in Europe, including those which were used in Finland. Kärkkäinen (2005) compared the performance of tree-level biomass models (Hakkila 1979, Marklund 1988, Issakainen 1988, Finér 1989, Hakkila 1991, Korhonen & Maltamo 1990, Laiho 1997). Repola et al. (2007) developed biomass equations for above- and below-ground tree components of Scots pine, Norway spruce and birch using data collected throughout Finland.

The climate and forest vegetation in Sweden, Norway, European Russia and other nearby countries are similar to those in Finland. It is useful both ecologically and in silvivultral practice to compare the forest biomass in these areas and illustrate its pattern in relation to the influential factors by means of meta-analysis.

2 AIMS OF STUDY

The overall aim of the dissertation is, 1) to compare different estimation methods based on investigations into the tree biomass in boreal Finnish stands, and 2) to show the pattern of the tree biomass accumulation with stand age in southern Finland.

Studies were conducted in a 30-year-old Scots pine stand and a 130-year-old mixed Norway spruce and Scots pine stand in southern Finland. The pattern of variation in annual stem biomass increment and the relation to the tree ring width were studied in 130-year-old trees (Study III). We quantified the vertical distribution of epiphytic lichen biomass on the Norway spruce and Scots pine trees, measured the amount of lichen litter on the forest floor and estimated the lichen biomass at stand level (Study I). In Study II, our objective was to present the distribution of tree biomass separately for needles, branches, stems and roots in the young Scots pine stand. In the final study (Study IV), the objective was to compare different approaches for estimating the dry mass of branches and needles at tree and the stand in the 130-year-old stand.

Based on a data set compiled from the studies previously published (Appendix 1), a meta-analysis was conducted to compare the potential of tree biomass accumulation in southern Finland with that in the nearby Sweden and Russia.

3 METHODOLOGY

3.1 Study forests

The forests studied are located in southern Finland (61°50' N, 24°22' E) in a region with a mean annual temperature of 2.9 °C and annual precipitation of 709 mm. Two sample stands were selected, one 130-year-old mixed Norway spruce - Scots pine stand (Mature-Stand), and a 30-year-old pure Scots pine stand (Young-Stand). There is about a 4-km distance between the two stands.

Mature-Stand was a naturally established mixed Norway spruce and Scots pine stand. The site lay on a south-facing slope with an average inclination of 3.4% and a mean elevation a. s. l. of 152 m. The forest site type changed along the slope, from dry VT on the top of the slope, over a mesic MT to moist OMT at the bottom (site type nomenclature according to Cajander (1949)). Correspondingly, the groundwater table level during growing seasons ranged between 4 and 10 m. In the middle part of the slope, a plot (30 × 30 m) was set up. Based on the survey of trees in the plot, stand density was 792 stems ha^{-1} (589 spruce and 203 pine trees, respectively), and the overall stem volume was 240 m3 ha^{-1}, of which 63% was Norway spruce and 37% Scots pine. Tree age varied from 100 to 140 years. According to silvicultural record, the stand was almost not disturbed by forestry management.

The young stand (Young-Stand) was established by sowing Scots pine after prescribed burning and scarification in 1962. A sample plot (893 m^2) was set up in the early 1990s. The soil on the site was podzolized glacial till soil (Study II). The density was 2093 stems ha^{-1} with a mean height of 10.2 m and a stem volume of 119 m^3 ha^{-1} in 1995 when the investigation was carried out.

3.2 Investigations in Mature-Stand

3.2.1 Selection of sample trees

In Mature-Stand, all trees in the plot were tallied by DBH class (1 cm). Because of highly varying size, spruce trees were stratified into three size groups: understorey (DBH < 15 cm), sub-dominant (DBH = 15-21 cm), and dominant trees (DBH > 21 cm). For each class, one sample tree having mean DBH and H of respective class was selected, one dominant (DS), one sub-dominant (MS) and one understory spruce (SS) (Table 1) (Study I, III and IV). Among the pine trees, all being dominating crown layer trees and consequently rather uniformly sized, we selected only one average dominant tree (AP) randomly based on mean DBH and H of all pines in the stand.

The sample trees were felled onto a large tarpaulin, to enable quantitative harvesting of the selected tree compartments. After felling, the stem of each tree was partitioned into 2-m sections starting at the highest point of the root neck of the tree, and the remaining top section. A 3-cm-thick disc was cut from lower end of each bolt and at the stem height of 1.3 m (Study I and IV).

Table 1. Age and dimensions of sample trees. Age is measured by counting the rings at the root neck of each sample tree (Study IV).

Sample trees	Age (years)	DBH (cm)	Height (m)	HPDB[a] (m)	HPLB[b] (m)	Crown width (m)	NLB[c]	TBNA[d] (cm^2)
SS	106	12.3	13.5	3.12	7.6	3.4	67	43.4
MS	133	18.6	19.9	2.1	3.9	3.9	119	181.8
DS	131	24.5	23.4	6.0	13.8	4.1	194	326.4
AP	137	28.8	24.1	6.0	16.0	5.7	84	310.9

[a]Height position of first dead branch; [b]Height position of first living branch; [c]Number of living branches; [d]Total basal neck area of living branches.

3.2.2 Measurement of annual stem biomass increment

In the laboratory, the disks were stored in a cold-room at –4 °C. The width of each tree ring was measured in four radial directions to an accuracy of 0.01mm. After the rings of a disc were measured, the mean width was calculated from the four measurements based on the values of the four facings. On the basis of tree ring data, annual stem biomass increment for each tree was calculated. The calculation has been fully described in Study III.

3.2.3 Determination of biomass of individual trees

For each sample tree, the stem dry mass was determined in three ways: i) by direct weighing (StemW), ii) by applying allometric functions of Marklund (1988) (StemM), and iii) by applying stem form functions for volume (StemF).(Study IV).

The dry mass of branches and needles were estimated in four ways: i) by direct weighing (BranchW, NeedleW), ii) by systematic sampling (BranchS, NeedleS), iii) on the basis of average branch (BranchA, NeedleA), and iv) by applying the allometric functions of Marklund (1988) (BranchM, NeedleM).

The root and stump dry mass was estimated in two ways: i) by direct weighing (RootW, StumpW), and ii) by applying the allometric functions of Marklund (1988) with DBH as an independent variable (RootM, StumpM) (Study IV). Except for the stump (StumpW), the roots were sorted in three groups, less than 2 mm, 2–20 mm, and over 20 mm, respectively denoting fine (FRootW), medium (MRootW) and coarse (CRootW) (Study IV).

Each method mentioned above has been fully described in Study IV.

3.2.4 Determination of tree biomass at stand level

The biomass of the trees was determined in five ways: i) by partial harvesting (StandW), ii) on the basis of sample trees (StandS), iii) by applying the allometric functions of Marklund (1988) (StandM), iv) by applying stem form functions for stem volume (StandF), and v) by systematic sampling of roots (StandRootS) (Study IV).

Among the five methods, the first one measured only the amount of above-ground biomass and the last one only estimated the dry mass of root fractions smaller than 2 mm and those between 2 and 20 mm.

3.2.5 Measurement of epiphytic lichen biomass

Four lichen species (or genus) were indentified in the stand, namely, *Hypogymnia physodes,* *Platismatia glauca, Bryoria* spp., and *Pseudevernia furfuracea*. For each lichen species (or genus) on the harvested sample tree, the mass was measured on sample branches. these values were scaled up for each tree and then to the satnd (Study I). The lichen on the litter branches was estimated based on litter branches collected from 70 quadrates (20 × 20 cm), which were systematically arranged within the 30 × 30 m plot (Study I).

3.2.6 Comparison among estimates

In order to compare the biomass estimates obtained by different methods, the values resulting from direct weighing were used as the base line (see Table 2), and a percent deviation from the observed values was calculated as follows:

Percent deviation (%) = $(M_E - M_W) / M_W \times 100$

Where M_E is estimated dry mass and M_W the corresponding dry mass determined through direct weighing.

3.3 Investigations in Young-Stand

3.3.1 Selection of sample trees

Based on DBH distribution of all trees in the sample plot, nine sample trees were selected for estimating the biomass of needles, branches and stem (Table 2). The sample branches were systematically selected for each sample tree, and the dry mass of the branches and its needles were measured (Study II). Based on the data from the sample branches, linear regression models between branch cross-sectional area and the dry mass of branches (and needles) were established for branch (and needle) mass for each sample tree (see Study II). For each sample tree, the dry mass of various components (needles, branches, stem) were measured to obtain the allometric functions in relation to stem cross-section area at breast height (ABH) (Study II).

In addition, five sample trees were selected for estimating the below-ground biomass (Table 3). The stump and roots were carefully excavated, and the samples were collected (Study II). All sample materials were oven-dried at 60 ºC for 24 hours. Based on the data from the sample trees, allometric functions for root biomass were established in relation to ABH of sample trees.

Table 2. Diameter at breast height (DBH), stem cross-section area at breast height (ABH), height (m) and stem dry mass (kg) of sample trees in Young-Stand.

Sample tree	DBH (cm)	ABH (cm^2)	Height (m)	Stem dry mass (kg)
#37	6.4	32.2	7.57	6.94
#213	7.8	47.8	9.95	12.06
#234	8.5	56.7	7.75	10.33
#36	8.5	56.7	8.37	14.74
#151	8.8	60.8	9.85	15.44
#134	9.3	67.9	9.95	17.25
#4	12.0	113.0	12.45	30.34
#172	14.1	156.1	11.47	42.55
#233	16.9	224.2	11.25	52.98
Mean(± sd)	10.3 (± 3.4)	90.6 (± 20.9)	9.85 (± 1.70)	22.51 (± 15.93)

Table 3. Diameter at breast height (DBH) and height (m) of sample trees for estimating the mass of roots and stump in Young-Stand.

Sample tree	DBH (cm)	Height (m)	Stump (kg)	Roots (kg)	Below-ground biomass (kg)
R1	8.2	9.0	2.23	2.28	4.52
R2	15.4	11.2	7.88	12.78	20.66
R3	9.7	10.9	6.35	4.23	10.57
R4	11.7	11.3	4.66	2.54	7.20
R5	6.5	8.5	1.67	1.16	2.80
Mean	10.3	10.17	4.56	4.60	9.16
(± sd)	(± 3.4)	(± 1.32)	(± 2.65)	(± 4.70)	(± 3.16)

3.3.2 Estimation of tree stand biomass

At the stand level, tree biomass was estimated in three ways. First, the simple linear regression models for sample tree dry mass of branch, needle, stem and roots based on ABH were established, respectively, and applied to calculate the biomass of respective components at the stand level (StandR) (Study II). Second, tree biomass was calculated using the allometric functions of Marklund (1988) (StandM). Third, the stem volume of trees was calculated from the DBH of all trees in the plot according to Laasasenaho (1982), and then was conversed into the stem biomass using a factor of 0.34 kg dm^{-3} (StandF) (Study II).

3.4 A Meta-analysis of tree stand biomass

In order to compare the biomass values in this study with values of forests growing in a data set of Norway spruce and Scots pine forest biomass within an area of 58.00 - 62.13 ºN, 14 - 34 ºE (≤ 300 m a.s.l.) was compiled from values reported by Cannell (1982) and Helmisaari et al. (2002) (*see* Appendix 1). The data set included information about the geographical coordinates (latitude º; longitude, º; altitude, m), climate factors (mean annual temperature, MAT, °C, and annual precipitation, APP, mm), above-ground tree biomass (AGB) and total tree biomass (TTB) (Mg ha^{-1}). The information of stand age was provided in the original papers. The stands included in the data set grew in mineral soils and were not disturbed by forestry management (e.g. fertilization, thinning etc.).

In addition, the data collected in this study (Study II, Study IV) were included in analysis. The relationship between total tree biomass (or above-ground biomass) and stand age was modelled by regression technique. Different types of models were tried, but only one model was listed with higher the value of r^2 and fewer parameters to be used in the model.

4 RESULTS

4.1 Variation in annual stem biomass increment

For all four sample trees from the studied mature stand (Table 1), annual stem-biomass increment followed a sigmoid curve during the period of observation (from 1870 to 1994) (Fig. 1). The fitted stem biomass increment curves reached a maximum in the early 1980s for sub-dominant (MS) and understory (SS) spruce and dominant pine when the trees were about 100-year-old, but still appeared to increase for DS. In addition, there was condierable difference in the annual stem biomass increment among DS, MS and SS at the later stages of tree growth. For instance, the average annual stem-biomass increment for DS in the 1980's was 6 kg yr^{-1}, which was six-fold that for SS. DS and AP had a similar annual biomass increment at the later stages.

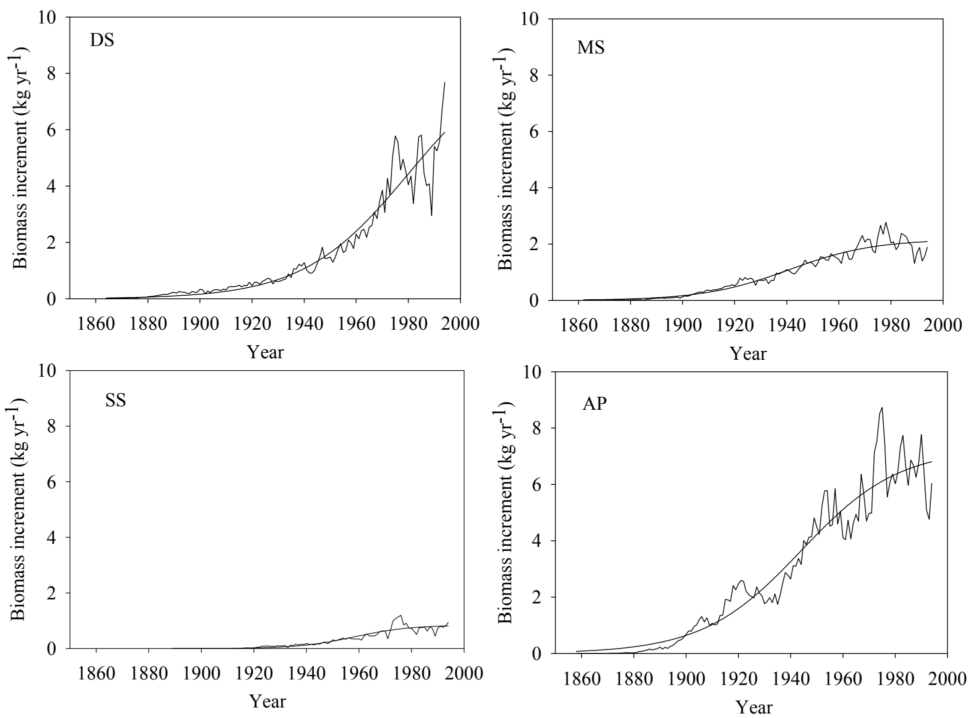

Figure 1. Variation of annual biomass increment (kg yr^{-1}) with age (yr) for dominant (DS), sub-dominant (MS), understory (SS) spruce, and average dominant pine (AP) in the stand. The model used is $y = a /(1+e^{-((x-x0)/b)})$; for DS, a = 8.8388, b = 20.1212, x_0 = 1979.87, r^2 = 0.96; for MS, a = 2.1671, b = 16.3821, x_0 = 1940.7996, r^2 = 0.97; for SS, a = 0.8410, b = 10.5421, x_0 = 1958.2832, r^2 = 0.94; for AP, a = 7.2792, b = 18.7736, x_0 = 1943.9614, r^2 = 0.97.

4.2 Forest biomass in Mature-Stand

4.2.1 Dry mass of individual trees

4.2.1.1 Measured biomass of individual trees

The total dry mass of sampled spruce trees in the studied mature stand ranged from 56 (understorey spruce) to 367 kg (dominant spruce). The dry mass of the dominant pine tree was almost 1.5 times that of the dominant spruce tree. Above-ground compartments constituted 75 to 87% of total tree biomass. The greatest above-ground fraction was found for the co-dominant spruce tree, which had the longest living crown (Table 4). The understory spruce tree had the greatest relative fraction of below-ground biomass. The high below-ground biomass fraction of the understorey tree was allocated to the coarse (> 20 mm) root compartment and the fractions of medium and fine roots were similar to the other spruce trees (Table 4).

Table 4. Dry mass (kg) of stem wood and bark (StemW), stump (StumpW), living branches (BranchW), dead branches, needles (NeedleW), coarse roots (CRootW), medium roots (MRootW) and fine roots (FRootW) obtained by direct weighing for sample trees in Mature-Stand (Study IV).

Sample trees	Above-ground biomass					
	StemW (wood)	StemW (bark)	BranchW	Dead branches	NeedleW	Subtotal
SS	29.1	3.4	2.8	4.2	2.4	41.9
MS	114.8	13.9	18.3	7.7	10.5	165.2
DS	202.5	23.6	26.0	20.8	19.2	292.1
AP	333.7	25.1	27.2	22.5	9.7	418.2
	Below-ground biomass					
	StumpW	CRootW	MRootW	FRootW	Subtotal	
SS	3.9	8.7	1.4	0.4	14.4	
MS	14.9	5.3	4.4	0.4	25.0	
DS	30.5	37.2	7.6	0.5	75.78	
AP	46.1	62.2	7.2	0.3	115.8	

4.2.1.2 Biomass estimated by different methods

The accuracy of the estimated sample tree needle biomass differed between the methods. The least accurate estimate (NeedleM) was more than twice the measured needle biomass in the case of the understorey spruce (Fig. 2 A). The estimates of branch material biomass varied even more: from less than a fifth of that measured, to more than two and a half times the measured mass (Fig. 2 B). The best estimates for branch biomass waere obtained by BranchS-1 and Stand-2. However, the variation among trees was substantial. Both single spruce tree models and the models for all spruces together overestimated the biomass of the medium spruce (see Table 4). On the other hand, estimates for the small spruce and particularly for the large spruce produced needle and branch biomass values reasonably close to the measured values. In the estimated results of three sample trees, no consistent variation was discerned between the two methods (NeedleS-1 vs. NeedleS-2; BranchS-1 vs.

BranchS-2) (Fig. 2 A, Fig. 2 B). For the sample pine tree, the models based on the NeedleS-1, NeedleS-2, BranchS-1 and BranchS-2 produced estimates well within ± 10% of measured values.

The estimates based on average branch (NeedleA and BranchA) were inaccurate and varied among the sample trees randomly between low and high estimates (Fig. 2). In three of four cases the needle biomass was overestimated, and for branch material the method yielded both over- and underestimations. However, based on the average branch method (NeedleM and BranchM), medium spruce needle and branch material biomass was underestimated.

Estimates based on the allometric functions of Marklund (1988) (NeedleM and BranchM) overestimated living biomass fractions for four sample trees. Nonetheless, except for the small spruce whose branch and needle mass was strongly overestimated, estimates were no worse than those obtained by the average branch method (Fig. 2 A) and (B)). The mass of dead branches was estimated to be less than one-fifth of the measured mass (Fig. 2 C).

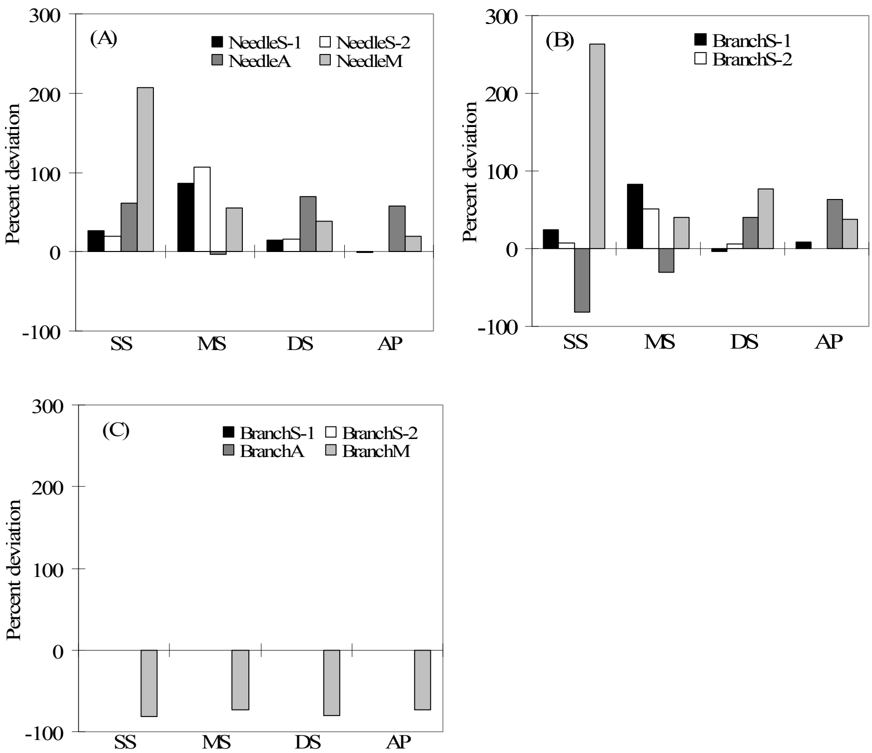

Figure 2. Percent deviation (%) for estimated dry mass of needles (NeedleS–1, NeedleS–2, NeedleA and NeedleM) (A), living branches (BranchS–1, BranchS–2, BranchA and BranchM) (B), and dead branches (BranchM) (C) on the baseline obtained by direct weighing (NeedleW, BranchW) (*see* Table 4) in the sample trees. The Percent deviations were calculated on the basis of the formula: $(M_E - M_W) / M_W \times 100$, where M_E is any estimated dry mass and M_W the corresponding dry mass fraction determined by direct weighing.

Stem biomass estimated based on volume and wood density closely resembled the measured values for the spruce trees (Fig. 3). Only for the co-dominant spruce tree was the estimate low, by somewhat more than one-tenth. In the case of the pine tree, stem mass was underestimated by one-fourth (Fig. 3). Estimated based on the allometric functions (Marklund 1988), however, underestimate both stem and stump compartments. In the case of the coarse root compartment, the outcome was highly variable among sample trees; coarse roots for the small spruce and pine trees were estimated correctly, while the estimate was extremely high for the medium spruce tree.

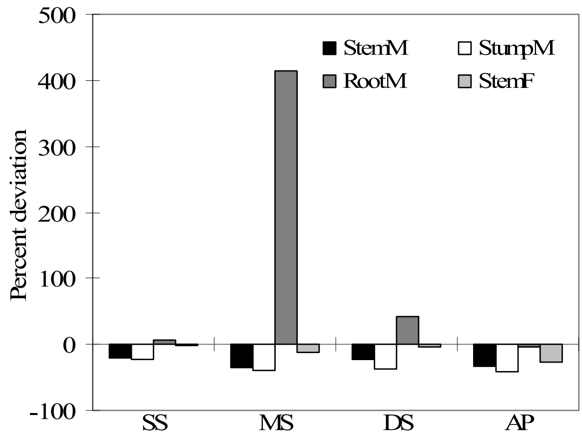

Figure 3. Percent deviation (%) for dry mass of stem (StemM, StemF), stump (StumpM), and coarse roots (RootM) estimated by allometric functions of Marklund (1988) and stem form functions by Laasasenaho (1972) on the baseline obtained by direct weighing (StemW, StumpW and RootW) of the sample trees (*see* Table 4). The Percent deviations (%) were calculated as: $(M_E - M_W) / M_W \times 100$, where M_E is any estimated dry mass and M_W corresponding dry mass fraction determined through direct weighing. For RootM, the root means the coarse roots with diameter ≥ 2 mm.

4.2.2 Tree biomass in the stand

4.2.2.1 Measured tree biomass

Above-ground biomass (stumps excluded) determined by weighing upon partial harvest method (StandW) totalled 170.8 Mg ha^{-1} (Table 5). Total above-ground biomass was distributed evenly between the two tree species (54 to 44%). The crown compartment of spruce, however, was more than double that of pine, while the stem compartment of pine was 1.5 times that of spruce.

Table 5. Above-ground biomass of Scots pine and Norway spruce based on the partial harvesting method (StandW) in Mature-Stand (Mg ha^{-1}).

Tree species	Crown[a]	Stem	Total in stand
Scots pine	8.2	85.0	93.2
Norway spruce	19.6	58.0	77.6
Total in stand	27.8	143.0	170.8

[a] Branches and needles combined.

Table 6. Root biomass by soil layer measured on the basis of core samples (StandRootS). Root fractions less than 2 and 2-20 mm are respectively denoted fine and medium roots (Mg ha^{-1}).

Soil layers	Woody medium roots	Woody fine roots	Non-woody fine roots	Total
Humus layer	4.8	3.3	2.8	10.9
Mineral soil 0-20 cm	3.5	6.1	1.1	10.6
Mineral soil 20-40 cm	1.3	1.9	0.1	3.3
Mineral soil 40-60 cm	1.5	2.3	0.1	3.9
Total in stand	11.1	13.7	4.0	28.8

Root biomass (roots less than 20 mm) in the humus layer and 0–60-cm mineral soil layer totalled 28.8 Mg ha^{-1} (Table 6). Most of the roots were woody roots (86%). The majority of the roots were in the humus layer and top 20 cm mineral soil.

4.2.2.2 Estimated tree biomass

Based on the sample tree method (StandS), the estimated stand biomass including medium and fine roots totalled 239.9 Mg ha^{-1}. Stand biomass estimated using the allometric functions of Marklund (1988) while allometric functions of Marklund (1988), StandM, produced an estimate of 183 Mg ha^{-1} excluding fine roots (Table 7). The above-ground biomass estimated by StandS and StandM was 189.8 and 141.4 Mg ha^{-1} (Table 7), respectively, and the measured value (170.8 Mg ha^{-1}) (Table 6) by StandW was between these values.

The biomass of the stump and below-ground component represented a substantial fraction of the total stand biomass (21%) (Table 7). Exclusion of fine roots would create only a minor error in the estimate as they amounted to only 0.5% of the total. However, the medium and fine root biomass (4.0 and 1.3 Mg ha^{-1}) estimated on the basis of StandS (Table 7) was much lower in comparison to those (11.1 and 13.7 Mg ha^{-1}) calculated from StandRootS in the stand (Table 6). These data show that StandS underestimated the medium and fine root biomass more than StandRootS.

There was no estimate of the below-ground biomass by StandW in this study. In the other two estimates, the below-ground biomass (including the roots and stump) was 21% of the total. If such a factor 21% was applicable in StandW, the below-ground biomass should be 45.4 Mg ha^{-1} and total tree biomass 216.2 Mg ha^{-1}.

4.2.3 Biomass of epiphytic lichens

The average lichen biomass on the trees examined was1.63 Mg ha^{-1} and the litter lichen was around 0.09 Mg ha^{-1} or one twentieth of the aerial biomass (Study I). The biomass basis of lichens on trees and in litter decrease in the order, *H. physodes* > *P. glauca* > *Bryoria* spp. > *P. furfuracea* (Table 8).

Table 7. Tree biomass in the stand determined by means of the sample tree method (StandS), allometric functions of Marklund (1988) (StandM) and volume-mass conversion (StandF) (Mg ha^{-1}). Roots < 2, 2-20 and over 20 mm in diameter are respectively denoted fine, medium and coarse roots.

	Above-ground biomass			Below-ground biomass					Grand total
	Crown[a]	Stem	Total	Stump	Coarse roots[b]	Medium roots	Fine roots	Total	
	StandS								
Scots pine	14.9	90.3	105.2	11.6	15.6	1.8	0.1	29.1	134.3
Norway spruce	19.0	65.6	84.6	8.5	9.0	2.2	1.2	20.9	105.5
Total	33.9	155.9	189.8	20.2	24.6	4.0	1.3	50.1	239.9
	StandM								
Scots pine	13.6	59.7	73.3	6.9	15.0	-	-	21.9	95.2
Norway spruce	22.5	45.8	68.3	5.1	14.4	-	-	19.5	87.8
Total	36.1	105.6	141.7	11.9	29.4	-	-	41.3	183.0
	StandF								
Scots pine	-	66.9	-	-	-	-	-	-	-
Norway spruce	-	34.8	-	-	-	-	-	-	-
Total	-	101.7	-	-	-	-	-	-	-

[a] The crown indicates the branches and needles combined.
[b] For StandM, the coarse roots should include the coarse roots and medium roots obtained by the sample tree method (StandS).

Table 8 Lichen biomass in the Mature-Stand (Mg ha^{-1}) (Study I).

	H. physodes	*P. glauca*	*Byroria* spp.	*P. furfuracea*	Total
Lichens on trees[a]	1.21	0.27	0.13	0.02	1.63
Lichens in litter[b]	0.068	0.016	0.003	0	0.088
	(± 0.007)	(± 0.004)	(± 0.001)		(± 0.009)

[a] Figures in parentheses % of total; [b] Mean (± s.e.) (n = 70).

4.3 Tree biomass in Young-Stand

4.3.1 Dry mass of individual trees

For individual trees in Young-Stand the mean stem mass was 22.51 kg (Table 2), the mean stump mass 4.56 kg and mean root mass 4.60 kg (Table 3). The belowground component was 29% of the total tree mass. As shown in Table 2, there was considerable variation in stem and root mass among individual trees. The range for stem biomass was 6.94–52.98 kg, 1.67–7.88 kg for stump, and 1.16–12.78 kg for roots. This shows that a differentiation had occurred among individual trees in this, even-aged artificially regenerated stand.

4.3.2 Allometric equations for tree biomass

The relationships between ABH of sample trees and the dry mass of needles, branches, stem and roots of the sample trees were well described with a linear model (Table 9). All models were significant ($p < 0.001$), and the r^2 was higher than 0.95 except for the root model.

Table 9. Summary of regression equations for needle, branch, stem and root biomass (kg) (*y*) against ABH (cm^2) (*x*) in Young-Stand. Linear model used is $y = a + bx$, where *a* is intercept.

Biomass component	Regression equations	*p*	*n*	r^2
Needles	$y = 0.1628 + 0.0233x$	< 0.001	9	0.96
Branches	$y = -1.2211 + 0.056x$	< 0.001	9	0.96
Stem	$y = -0.2032 + 0.2508x$	< 0.001	9	0.98
Roots	$y =-0.78604 + 0.1096x$	< 0.001	5	0.87

4.3.3 Tree biomass at stand level

The total tree biomass estimated using the above regression equation was 72.5 Mg ha^{-1}, of which above-ground biomass occupied 83% and below-ground biomass 17% (Table 10). Among aboveground components, stem was the largest fraction (63%) and needle the smallest one (7%). StandM gave an estimate of total tree biomass, similar to that by StandR, but the two methods displayed different estimates on the amount of stem and root. With Standf, the stem mass was estimated to be 41.5 Mg ha^{-1}, about 10% less than that estimated by the regression equation, and the total biomass was 68.1 Mg ha^{-1}.

Table 10. Tree biomass (Mg ha^{-1}) estimated by the means of regression equations (Table 9) and volume-mass conversion method (StandF) and allometric functions of Marklund (1988) (StandM) in Young-Stand.

	Above-ground biomass (Mg ha^{-1})			Below-ground biomass	Total biomass
	Needles	Branches	Stem	(Mg ha^{-1})	(Mg ha^{-1})
StandR	5.1	9.0	45.9	12.5	72.5
StandF[a]	-	-	41.5	-	(68.1)[b]
StandM	5.4	9.6	41.0	16.6	72.7

[a] The stem volume of trees in the stand was calculated on the basis of Laasasenaho (1982) and the mass-volume conversion factor was 0.34 kg dm^{-3}.
[b] Total biomass was 68.1 Mg ha^{-1} with the stem mass estimated by volume-mass conversion.

4.4 Tree stand biomass in southern boreal zone

Using data from the boreal zone (58.00-62.13 ºN, 14-34 ºE, ≤ 300 m a.s.l.) (Appendix 1), including southern Finland, northern Sweden and western Russia, the relationship between total tree biomass (or above-ground biomass) and stand age was modelled with a sigmoidal curve (Fig. 4, Table 11). At the stage of mature forests, the maximum tree biomass in a stand was c. 250 Mg ha^{-1} in the Norway spruce forests in Karelia (Kazimirov & Morozova 1973), and the lowest value occurred in the two Scots pine stands in Sweden where the sites had an altitude of 300 m a.s.l. (Albrektson 1980) (Fig. 4 A). At the stage of mature forests, the mean value of above-ground tree biomass was *c.* 150 Mg ha^{-1} with the maximum of *c.* 200 and the minimum of c. 83 Mg ha^{-1} (Fig. 4 B). For Mature-Stand in this study, both the total and above-ground tree biomass estimated was in the middle position of the biomass range.

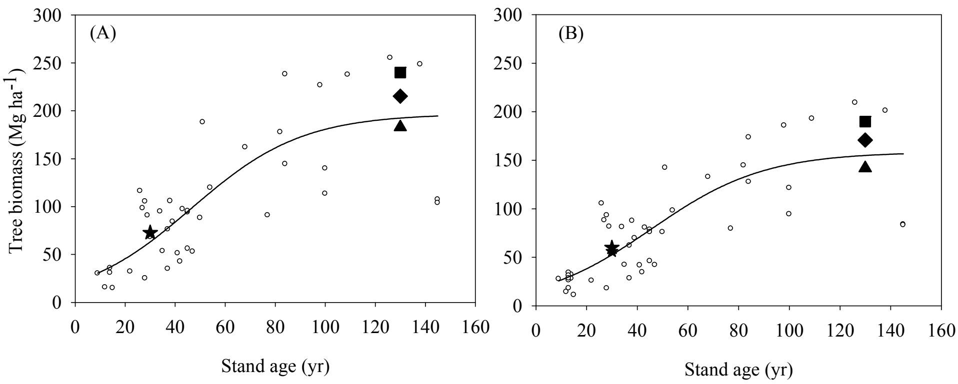

Figure 4. Relationship between total (A) and above-ground (B) tree biomass estimates and stand age for Scots pine and Norway spruce forests across boreal zone (58.00-62.13 °N, 14–34 °E, ≤ 300 m a.s.l.). In the figure, data represented by the open circles are based on the data set (Appendix I). The solid stars represent data of tree biomass estimated by StandR and StandM, respectively, in Young-Stand (Study II), and the others from Study IV (solid square for StandS, solid diamond for StandW and solid triangle for StandM). The models and parameters are listed in Table 11.

Table 11. Summary of regression models for total and above-ground biomass (y) against stand age (x) ($y = a/(1+\exp(-(x-x_0)/b))$) (*see* Fig. 4).

	Coefficient	SE	*t*	*p*
Total biomass (R^2 = 0.65, p < 0.001, n = 46)				
a	196.8449	17.3143	11.3689	<0.001
b	22.1404	6.0594	3.6539	=0.007
x_0	46.5823	6.7749	6.8757	<0.001
Aboveground biomass (R^2 = 0.68, p < 0.001, n = 50)				
a	158.4236	13.2907	11.9199	<0.001
b	22.3212	5.8866	3.7919	=0.004
x_0	45.6277	6.4341	7.0916	<0.001

The regression curve increased almost in a linear manner from a stand age of 10 to 80 years, and then levelled off, with a maximum of *c.* 180 Mg ha^{-1} at the age of 140 years (Fig.4 A). The tree biomass was still at the fast-growing stage in Young-Stand, but at the slow-growing stage in Mature-Stand (Fig. 4). The tree biomass estimated in Young-Stand (68.1–72.5 Mg ha^{-1}, the star) was close to the mean in the stands of similar age (Appendix 1). The tree biomass in Mature-Stand was estimated to be about 183, 216 and 240 Mg ha^{-1} by Marklund's functions (StandM), partial harvesting (StandW), and sample-tree based method (StandS), respectively. Compared with the regression mean value, whereas Marklund's functions and the partial harvesting gave closer value, and the sample-tree based method yielded a higher one (Fig. 4).

5 DISCUSSIONS

5.1 Comparison of biomass estimation methods at tree level

In assessing biomass estimation methods, two main aspects should be taken into account: accuracy and cost-efficiency. In this study different methods to estimate the biomass of different components of a tree: needles, branches, stem, roots, were investigated (Study IV). The direct weighing method results were used as the base line as the base line, the regression technique gave relatively the closest estimate among the methods. However, in terms of time and labour saving, although the allometric functions of Marklund (1988) did not give ideal results, but these functions require only some calculations based on DBH of the sample trees. The average sample branch method and regression technique used approximately the same number of sample branches: 69 and 63 (Study IV). Based on these considerations, the application of the regression technique based on sample branches would be the optimum choice for estimating the dry mass of branch and foliage materials of a tree.

The average sample branch method is not an ideal technique either in terms of accuracy or cost-effect, the average branch method dose not consider the physiological function of sapwood (Study IV). According to the pipe model theory (Shinozaki et al. 1964), branch and needle mass are not dependent on the total neck cross-sectional area of the branch, but are explained rather by the fraction of sapwood. Fang and Wang (2001) noted that biomass estimates can be biased because direct sampling tends to be carried out on specimens that are slightly better than average.

It is not surprising for that Marklund's (1988) functions did not return accurate biomass estimates for individual sample trees (Study IV). Any allometric function established on samples collected over a wide area has limitations when applied to other stands. The allometric functions of Marklund (1988) were mainly designed for large-scale tree biomass estimation (Kärkkäinen 2005), but they were based on tree-level biomass estimation. In this study, those functions were applied to estimate the biomass of individual trees as a comparison. An interesting phenomenon was that Marklund's (1988) functions gave higher estimates on the biomass of branches and needles for all four sample trees (Fig. 2 A, B) and lower estimate on that of the dead branches (Fig. 2 C), stem and stump (Fig. 3). In this sense, the possible overestimates on branch and needle biomass by Marklund's (1988) functions should be taken into account even if these functions are applied at large-scale.

Stem volume is also often used as the basis when calculating BEF values (Fang et al. 1998, Fang and Wang 2001, Lehtonen et al. 2004). In the mature stand (Mature-Stand) in this study, we obtained almost correct dry mass estimates for the stem component of the spruce trees, but the estimate for the pine tree exceeded the true value by one-fourth (Study IV). It is obvious that stem volume would be a reliable independent variable for dry mass estimation assuming that appropriate density values are available.

Measurement of biomass is, by definition, the process of direct measurement of the mass of a tree or its component. The estimation of biomass involves the extraction of some sub-sample followed by the calculation of the mass of the respective component (Satoo 1982, Parresol 1999). The process of collecting complete samples of trees for weight measurement is time consuming and expensive, consequently, direct measuring of the mass of biomass is seldom performed. The majority of reported values are estimates based on sub-samples selected by some procedure from the respective tree compartment. Such sub-samples are often selected arbitrarily, and the estimates and variances from such samples are known to be biased. The most appropriate approach would be randomised sampling of trees, which would produce truly unbiased estimates (Cunia 1979, Valentine et al. 1984).

5.2 Comparison of biomass estimation methods at stand level

When different estimation methods were applied in estimating forest biomass worldwide, attention was paid early on to test the errors of estimation. For instance, Ovington et al. (1967) applied three methods (unit area, average tree and regression analysis method) to estimate the tree biomass in a 0.081-ha plot within a *Pinus radiata* plantation. In the plot all trees were harvested to measure the dry weight of different components as a baseline for comparison with the three estimation methods. In Ovington's et al. (1967) study, the average tree method was similar to StandS method used in Mature-Stand (Study IV) and the regression analysis to StandR applied in our Young-Stand (Study II). The results showed that the average tree method and regression analysis method were more satisfactory than the unit area method (Ovington et al. 1967). In this case, the average tree method needed fewer sample trees compared with regression analysis method. Owing to this advantage, the average tree method has been popular among Chinese (e.g. Zhai 1982) and Indian researchers (e.g. Rana et al. 1988). As discussed below, however, the average tree method in the present study yielded tree biomass estimate that were inconsistent with the measured value.

As shown in Kärkkäinen's (2005) results, the allometric functions of Marklund (1988) are applicable to large-scale tree biomass estimation in Finland, and were even performed better than that of Hakkila's (1979, 1991) models that were established on the basis of sample trees collected in Finland. However, Kärkkäinen (2005) cautioned that uncertainties arise when Marklund's (1988) functions are applied on a small scale. In this study, Marklund's (1988) functions underestimated the tree biomass compared with the measured baseline values for the Mature-Stand. But we have to point out that Marklund's (1988) functions a little overestimated the crown biomass (+9 Mg ha^{-1}), but underestimated the stem biomass (-38 Mg ha^{-1}) in comparison with measured values.

In the mature stand (Mature-Stand) in this study, the sample tree method (StandS) returns an overestimate of approximately 10% with the measured value (SatndW). This is consistent with the observation that sample-tree-based measurements that can be biased by subjectivity may overestimate biomass (Fang and Wang 2001). In addition, as the biomass of pine trees in the forest is based on only one sample tree by weighing, non-normality of the tree breast height cross-sectional area in this single sample tree may seriously bias the overall estimate. Other compartments (spruce stem and crown, pine stem) are approximately within ± 10% of the measured values.

For the young stand (Young-Stand) in this study there was no base line for assessing different methods, but a comparison among the different estimates is also interesting. Both the regression models, StandR and StandM (Marklund's functions), gave a similar estimate on needle and branch biomass, but Marklund's functions (StandM) yielded a lower estimate (about -10%) for the stem biomass and a higher one (+33%) for below-ground biomass (Table 10). The soil is shallow at the young stand which might have resulted in a smaller fraction of tree root biomass in total tree biomass. However, the allometric functions of Marklund (1988) were established on the basis of nationwide sample trees, representing the average status of site conditions and respective tree growth, and display an inability of reflecting such a specific site condition (Kärkkäinen 2005).

Helmisaari's et al. (2007) results showed that, Norway spruce fine root (< 2 mm diameter, 30 cm in depth) biomass varied between 1.84 and 3.70 Mg ha^{-1} from southern to northern Finland and total fine root biomass of all tree species plus the total biomass of understory roots and rhizomes (< 2 mm diameter) ranged between 2.07 and 5.52 Mg ha^{-1}. For Scots pine stands, corresponding values were 1.49 vs. 3.86 Mg ha^{-1} and 2.30 vs. 4.93 Mg ha^{-1}. In the present study, the fine root biomass (< 2 mm diameter, 60 cm in depth) in Mature-Stand was 1.30 Mg ha^{-1} estimated by direct measurement of sample trees (StandS) (only fine roots for pine and spruce) (Table 7) and 17.7 Mg ha^{-1} (13.7 Mg ha^{-1} for woody roots and 4.0 Mg ha^{-1} for non-woody roots) by systematic sampling measurement (StandRootS) (Table 6). Compared with Helmisaari's et al. (2007) result, our StandRootS values were much higher. This difference in the fine root estimate between StandRootS in the present study and Helmisaari et al. (2007) is at least partly explained by its difference in the sampling depth: 60 cm for StandRootS and 30 cm for Helmisaari's et al. (2007).

5.3 Variation of annual stem biomass increment with tree age

The pattern of variation in above-ground net primary productivity (ANPP) with age and the influential factors have been intensively discussed at stand level (*see* Gower et al. 1996). There is a distinct difference in the age of forests when ANPP peaks in different climate zones. For instance, ANPP peaks at age of 70-year-old in Norway spruce stands (boreal area) but peaks at age of 30 –year-old in *Pinus elliotii* stand (temperate area) (Gower et al. 1996). Since annual stem biomass increment on individual trees is closely related ANPP in a stand, investigating the pattern of age-based variation in stem biomass increment is important to better understand of biomass accumulation at both tree level and stand level.

During the period of tree growth from a seedling to a mature tree, the variations in annual stem biomass increment are displayed in two ways (Fig. 1). First, the dry mass of stem produced per year generally increases year by year. This happens because more dry matter is produced yearly by photosynthesis, and consequently more can be allocated to stem growth. Second, there is inter-annual fluctuation in annual stem biomass increment which is mainly due to variation in environmental factors (e.g. climatic factors, competition among trees). In this study, we demonstrated not only an overall trend of variation in annual stem biomass increment in the Norway spruce and Scots pine during a period of about 130 years, but also differences in annual stem biomass increment among dominant, co-dominant and understory trees. In particular, the dominant spruce was still increasing its annual stem biomass at the age of 130 years, while the understorey (even co-dominant) spruce had reached a constant level.

5.4 Tree biomass accumulation in forests in southern Finland

On a broad geographical (e.g. continental or biome) scale, the maximum tree biomass is mainly associated with the prevailing climate (see Cannell 1982, Satoo 1982). On a local scale, the standing biomass in a stand varies with site factors, stand properties (e.g. age, density, species composition etc.), which may largely result from human activities. Given the tree species and environmental conditions, the accumulation of biomass in a stand is a saturating function of tree stand age (Sprugel 1984, Pare & Bergeron 1995). For instance, the model described by Bomann and Likens (1979) for biomass accumulation during stand development in northern hardwood forests stipulates that, following a large scale disturbance, tree biomass accumulates slowly at first, then more rapidly and then at a decreasing rate before reaching a stage of maximum standing biomass. Thereafter the biomass remains constant or declines slightly (Sprugel 1984, Pare & Bergeron 1995).

There are several papers on biomass investigations in Finnish forests, e.g. Mälkönen (1974), Paavilainen (1980), Finér (1989), Laiho & Laine (1997), Helmisaari et al. (2002). Of these papers, the works of Finér (1989) and Laiho & Laine (1997) were concerned with tree biomass on peatland, and their estimates were not used for a comparison with our estimates for the mineral soils. Helmisaari et al. (2002) carried out a study in three Scots pine stands at different stages of age in eastern Finland (62°47′ N, 30°58′E, 145 m a.s.l.), The estimated tree biomass was 14.94 Mg ha^{-1} for the sapling stand, 54.47 Mg ha^{-1} for the pole stage stand, and 139.70 Mg ha^{-1} for the mature stand. The biomass in the mature stands (Helmisaari et al. 2002) was smaller than the mean values for forests across the boreal zone (Fig. 5) and in the stands of this study.

The world's largest standing biomass ever estimated was up to more than 4000 Mg ha^{-1} in over 1000-year-old stands of coast redwood (*Sequoia sempervirens*) in the Pacific Northwest (Waring & Franklin 1979). In some tropical and subtropical forests, tree biomass up to more than 1000 Mg ha^{-1} is possible (see Cannell 1982). In boreal forests, the record in tree biomass accumulation was less than 300 Mg ha^{-1} according to Cannell (1982). In this study, in light of the pattern of variation in the annual stem biomass increment with tree age (Fig. 2), the annual stem biomass increment in Mature-Stand at age of 130 years should be the maximum for understorey and co-dominant spruces and dominant pine. At stand level in the study area, tree biomass accumulation seemed to approach its peak (220 Mg ha^{-1}) according to the tree biomass accumulation curve at the age of 120–150 years (Fig. 5). These data indicated that the maximum tree biomass in the forests of southern Finland might be 250 Mg ha^{-1} dry matter.

5.5 Epiphytic lichen biomass in boreal forests

Scotter (1962, 1964) reported an epiphytic lichen biomass of 0.15–0.23 Mg ha^{-1} in mature *Picea mariana* stands, and 0.09–0.47 Mg ha^{-1} in a stand of *Pinus banksiana* in boreal Saskatchewan. Trass (1965) recorded 0.40–0.48 Mg ha^{-1} of lichens on *Pinus sylvestris* in Estonia. In a mixed stand of *Picea abies* and *Betula pubescens* in northern Finland (66°22′N, 29°15′E), Havas & Kubin (1983) found 0.90 Mg ha^{-1} of lichen mass. Compared with these data for boreal forests, the lichen mass in our study (1.63 Mg ha^{-1}) is high. The main causes of this difference might be regional variation in the climate and stand conditions. For example, in the study of Havas & Kubin (1983), the stand density was 550 trees ha^{-1}, the height 16 m, the basal area 20 m^2 ha^{-1}, and the quantities of dead branches and living branches were 4.10 and 17.10 Mg ha^{-1}, respectively. For the stand investigated here, the mean tree height was 20 m, the density 881 trees ha^{-1}, and the basal area 31 m^2 ha^{-1}; the quantities of dead and living branches were 2.75 and 4.80 Mg ha^{-1} for the pine and the quantities of dead and living spruce branches 7.50 Mg ha^{-1} and 11.51 Mg ha^{-1} for the_spruce, respectively (Liu, unpublished data). Our stand is also subject to a higher annual mean temperature and precipitation. These data show that in our stand there is a much larger surface area of dead and living branches for lichens to grow on, and the microclimatic conditions might also be more favourable for lichens.

6 CONCLUSIONS

There is an increasing need for accurate estimation of forest biomass and associated carbon stocks at differing geographical scales. Over the last decades a variety of methods have been developed and applied to estimate forest biomass. For a rational utilisation of the biomass data published and a reduction of uncertainties in calculating the carbon storage in forests, the practicability and reliability of these methods in different conditions should be assessed. In this study, through the investigations of stand-based forest biomass in southern Finland and comparison with that of other studies both within Finland and across boreal zone, the main results obtained were as follows.

The tree biomass was estimated to be about 70 Mg ha^{-1} for a 30-year-old young stand and 200 Mg ha^{-1} for a 130-year-old mature stand. For the European boreal zone surrounding our study stands (58.00-62.13 ^{o}N, 14-34 ^{o}E, ≤ 300 m a.s.l.), the tree biomass accumulation in the stands followed a sigmoid curve with a mean maximum of about 200 Mg ha^{-1} (ranging from 100 to 250 Mg ha^{-1}) at the age of 130 years. The amount of tree biomass accumulated in the two stands of this study was of a medium level when compared with the biomass found in forests at corresponding stages of age in this region.

For the individual mature trees (130-year-old) in southern Finland, the annual stem biomass increment increased in relation to tree age following a sigmoid equation, and the fitting curves reached the maximum level (from about 1 kg dry matter yr^{-1} for understorey spruce to 7 kg dry matter yr^{-1} for dominant pine) when the trees were 100 years old).

Epiphytic lichen biomass is a minor but ecologically important component of stand biomass in boreal forests. In the study area, epiphytic lichen biomass was estimated to be 1.63 Mg ha^{-1} in the mature stand.

At tree level, the regression technique based on sample branches is an optimal method for estimating the dry mass of branch and foliage biomass when the accuracy and cost-effect are taken into account. At stand level, our study demonstrated that there are substantial differences among the methods used to estimate the dry mass of different components in a stand. The allometric functions of Marklund (1988) are useful for large-scale studies but when applied to specific stands, the results are reliable.

REFERENCE

Ahti, T. 1959. Studies on the caribou lichen stands of Newfoundland. Annales Botanici Societatis Zoologicae-Botanicae Fennicae Vanamo 30: 1–44.

Ahti, T. 1977. Lichens of the boreal coniferous zone. In: Seaward M.R.D. (ed.). Lichen ecology. Academic Press, London. p. 145–191.

Albrektson, A. 1980. Biomass of Scots pine (*Pinus sylvestris* L.). Amount, development, methods of mensuration, Report no. 2. Department of Silviculture, Swedish University of Agricultural Science, Umea, Sweden.

Andreev, V.N. 1954. Growth of forage lichens and methods of improving it. Geobotania 9: 11–74.

Attiwill, P.M. 1962. Estimating branch dry weight and leaf area from measurements of branch girth in Eucalyptus. For. Sci. 8: 132–141.

Attiwill, P. M. 1966. A method for estimating crown weight and stem diameter. Ecology 47: 795–804.

Bao, X., Chen, L., Chen, Q., Ren, J., Hu, Y. & Li, Y. 1984. The biomass of planted oriental oak (Quercus variabilis) forest. Acta Phytoecologia Et Geobotanica Sinica 8: 313–319.

Barber, V.A., Juday, G.P. & Finney, B.P. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668–673.

Baker, T.R., Phillips, O.L. & Malhi, Y. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10: 545–562.

Bhartari, S.K. 1986. Biological productivity and nutrient cycling in *Pinus patula* plantations of Darjeeling Hills. Indian Forester 112: 187–201.

Bohn, K.K. & Nyland, R.D. 2003. Forecasting development of understory American beech after partial cutting in uneven-aged northern hardwood stands. For. Ecol. and Manag. 180: 453–461

Bomann, F.H. and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York. 272 p.

Bonner, G.M. 1985. Inventory of Forest Biomass in Canada. Petawawa National Forestry Institute, Canadian Forest Service, Ontario.

Bouriaud, O., Bréda N., Dupouey J.-L. & Granier A. 2005. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. Can. J. For. Res. 35: 2920–2933.

Brandel, G. 1990. Volume functions for individual trees. Scots pine, Norway spruce and birch. Swedish University of Agricultural Sciences, Department of Forest Yield Research, Garpenberg. 183 p.

Brookhouse, M. & Brack C. 2008. The effect of age and sample position on eucalypt tree-ring width series. Can. J. of For. Res. 38: 1144–1158.

Brown, S., Gillespie A.J.R., Lugo A. E. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. For. Sci. 35: 881–902.

Brown, S. 1997. Estimating biomass and biomass change of tropical forests. A Primer. FAO Forestry Paper No 134. Rome.

Brown, S.L., Schroeder, P. & Kern, J.S. 1999. Spatial distribution of biomass in forests of the eastern USA. For. Eco. and Manag. 123: 81–90.

Cannell, M.G.R. 1982. World forest biomass and production data. Academic Press, Penicuik, Scotland. 391 p.

Cajander, A.K. 1925. The theory of forest types. Acta Forestalia Fennica 29: 1–108.

Cook, E.R. & Kairiukstis, L.A. (eds) 1989. Methods of Dendrochronology: Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht. 408 p.

Crow, T.R. 1971. Estimation of biomass in an even aged stand-regression and mean tree techniques. In: Young H.E. (ed.). Forest biomass studies. p. 35–50. University of Maine Press, Orono.

Cummings, W.H. 1941. A method for sampling the foliage of a silver maple tree. J. For. 39: 382-84.

Cunia, T. 1979. On tree biomass tables and regression: some statistical comments. In: Freyer, W.E. (ed.). Forest resource inventories, Workshop Proceedings, July 23–26. Vol 2: 629–642.

DeAngelis, D.L., Gardner, R.H. & Shugart, H.H. 1981. Productivity of forest ecosystems studied during the IBP: the woodlands data set. In: Reichle D.E. (ed.). Dynamic properties of forest ecosystems. p. 567-672. Cambridge University Press, Cambridge.

Drake, J.B., Knox, R.G., Dubayah, R.O., Clark, D.B., Condit, R., Blair, J.B. & Hofton, M. 2003. Above-ground biomass estimation in closed canopy Neotropical forests using lidar remote sensing: factors affecting the generality of relationships. Global Ecology and Biogeography 12: 147–159.

Edwards, R.Y., Soos T. & Ritcey R.W. 1960. Quantitative observations on epiphytic lichens used as food by caribou. Ecology 41: 425–431.

Eronen, M. & Zetterberg, P. 1996. Climatic changes in northern Europe since the late glacial times, with special reference to dendroclimatological studies in northern Finnish Lapland. Geophysica 32: 35–60

Esseen, P.-A. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications 6: 228–238.

Fang, J.Y., Wang, G.G., Liu, G.H. & Xu, S.L. 1998. Forest biomass of China: An estimate based on the biomass-volume relationship. Ecological Applications 8: 1084–1091.

— & Wang, Z.M. 2001. Forest biomass estimation at regional and global levels, with special reference to China's forest biomass. Ecological Research 16: 587–592.

Feng, Z., Wang, X. & Wu, G. 1999. Biomass and productivity of Chinese forest ecosystems. Science Press, Beijing. 345 p.

Finér, L. 1989. Biomass and nutrient cycling in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208.

Finnish Statistical Yearbook of Forestry. 2007. Finnish Forest Research Institute. SVT Agriculture, forestry and fishery. 436 p. (In Finnish with English summary).

Forsius, M., Kankaala, P., Karjalainen, T., Kellomäki, S., Laine, J., Lehtilä, A., Martikarnen, P., Ojala, A., Pingoud, K., Pipatti, R., Savolainen, I. & Silvola, J. 1996. Suomen kasvihuonekaasujen päästöt ja nielut. In: Kuusisto E., Kauppi L. & Heikinheimo P. (eds.). Ilmastonmuutos ja Suomi. SILMU. p. 179–196. Helsinki University Press.

Fournier, R.A., Luther, J.E., Guindon, L., Lambert, M.-C., Piercey, D., Hall, R.J., & Wulder M.A. 2003. Mapping aboveground tree biomass at the stand level from inventory information: test cases in Newfoundland and Quebec. Can. J. For. Res. 33: 1846–1863.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, London. 567 p.

Führer, E. 2000. Forest functions, ecosystem stability and management. Forest Ecology and Management 132: 29–38.

Gerson, U. & Seaward, M.R.D. 1977. Lichens-invertebrate associations. In: Seaward, M.R.D. (ed.). Lichen ecology. p 69–119. Academic Press, London.

Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A. & Munger, J.W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279: 214–217.

Gower, S.T., McMurtrie, R.E. & Murty, D. 1996. Aboveground net primary production

decline with stand age: potential causes. TREE 11: 378–382.
—, Krankina, O., Olson, R.J., Apps, M., Linder, S. & Wang, C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecological Application 11: 1395–1411.
Hakkila, P. 1979. Wood density surveys and dry weight tables for pine, spruce and birch stems in Finland. Communicationes Instituti Forestalis Fenniae 96(3). 59 p.
— 1991. Crown mass of trees at the harvesting phase. Folia For. 773: 1–24.
Hari, P. & Kulmala, L. 2008. Boreal Forest and Climate Change. Springer, Netherlands. 582 p.
Havas, P. & Kubin, E. 1983. Structure, growth and organic matter content in the vegetation cover of an old spruce forest in Northern Finland. Annales Botanici Fennici 20: 115–149.
Helmisaari, H.-S., Makkonen, K., Kellomaki, S. & Valtonen, E. 2002. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. Forest Ecology and Management 165: 317–326.
—, Derome, J., Nöjd, P. & Kukkola, M. 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiology 27: 1493–1504.
Hiura, T. 2005. Estimation of aboveground biomass and net biomass increment in a cool temperate forest on a landscape scale. Ecological Research 20: 271–277.
Hoen H.F. & Solberg B. 1994. Potential and economic efficiency of carbon sequestration in forest biomass through silvicultural management. Forest Science 40: 429–451.
Houghton, R.A., Lawrence, K.T., Hackler, J.L. & Brown, S. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Global Change Biology: 7, 731–746.
Husch, B., Miller, C.I. & Beers, T.W. 1982. Forest Mensuration. John Willey & Sons, New York. 456 p.
Huuskonen, S., Hynynen, J. & Ojansuu, R. 2008. Stand characteristics and external quality of young Scots pine stands in Finland. Silva Fennica 42: 397–412.
IGBP Terrestrial Carbon Working Group 1998. The terrestrial carbon cycle: Implications for the Kyoto Protocol. Science 280: 1393-1394.
Issakainen, A. 1998. Männyn, kuusen ja koivun juurakoiden biomassa ja ravinteet ojitetulla suolla. Helsingin yliopisto, suometsätieteen laitos. Tutkielma MMK-tutkintoa varten. 68 p.
Jacoby, G.C. D'Arrigo, R.D. & Davaajamts, T. 1996. Mongolian tree rings and 20th-century warming. Science 273: 771−773.
Karjalainen, K., Kellomäki, S. & Pussinen, A. 1995. Carbon balance in the forest sector in Finland during 1990–2039. Climate Change 30: 451–478.
Kauppi, P.E., Mielikäinen, K. & Kuusela, K. 1992. Biomass and carbon budget of European forests, 1971 to 1990. Science 256: 70–74.
Kazimirov, N.I. and Morozova, R.M. 1973. Biological cycling of matter in spruce forests of Karelia. Leningrad: Nauka, Lenigrad Branch, Academy of Sciences, U. S. S. R. 216 p.
Knops, J.M.H., Nash, III T.H., Boucher V.L. & Schlesinger W.L. 1991. Mineral cycling and epiphytic lichens: implications at the ecosystem level. Lichenologist 23: 309–321.
—, Nash, III T.H. & Schlesinger, W.H. 1996. The influence of epiphytic lichens on the nutrition cycling of an oak woodland. Ecological Monographs 66: 159–179.
Korhonen, K. & Maltamo M., 1990. Männyn maanpäällisten osien kuivamassat Etela¨-Suomessa. Metsäntutkimuslaitoksen tiedonantoja, Joensuun tutkimusasema 371.
Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated

threatened species to landscape and habitat changes. Scand. J. Forest Res. Suppl. 3: 27–37.

Kuusinen, M., Mikkola, K. & Jukola-Sulonen, E.-L. 1990. Epiphytic lichens on conifers in the 1960s to 1980s in Finland. In: Kauppi, P., Anttila P. & Kenttämies, K. (eds). Acidification in Finland. p 397–420. Springer-Verlag, Berlin.

Kärkkäinen, L. 2005. Evaluation of performance of tree-level biomass models for forestry modeling and analyses. Finnish Forest Research institute, Research papers 940, 2005.

Laasasenaho, J. 1982. Taper curve and volume functions for pine, spruce and birch. Comm. Inst. For. Fenn. 108: 1–74.

Laiho, R. 1997. Plant biomass dynamics in drained pine mires in southern Finland: Implications for carbon and nutrient balance. The Finnish Forest Research Institute, Research Papers 631. 54.

— & Laine, J. 1997. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. For. Ecol. Manage. 93: 161–169.

Lehtonen, A., Mäkipää, R., Heikkinen, J., Sievänen, R. & Liski, J. 2004. Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. For. Ecol. Manage. 188: 211–224.

— 2005. Estimating foliage biomass in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) plots. Tree Physiology 25: 803–811.

Levula, J., Ilvesniemi, H. & Westman, C. J. 2003. Relation between soil properties and tree species composition in a Scots pine–Norway spruce stand in southern Finland. Silva Fennica 37: 205–218.

Lieth, H. 1975. Modeling the primary productivity of the world. In: Lieth, H. and Whittaker, R. H. (eds.). Primary productivity of the biosphere. p 237-264. Springer-Verlag, New York.

Lilja, S. & Kuuluvainen, T. 2005. Structure of old Pinus sylvestris dominated forest stands along a geographic and human impact gradient in mid-boreal Fennoscandia. Silva Fennica 39: 407–428.

Liski, J. & Westman, C.J. 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. Biogechemistry 29: 183-197.

Liu, C.J., Guo, X.L. Xu, Z. 1985. A preliminary study on the root system of *Pinus tabulaeformis* and *Quercus variablis* mixed stand in Beijing region. Journal of Beijing Forestry College 7: 31–35.

— 1987. Studies on the biomass and nutrient cycling in *Pinus tabulaeformis* and *Quercus variablis* mixed stand in Xianshan area. Journal of Beijing Forestry University 9: 1–7.

Luther, J.E., Fournier, R.A., Hall, R.J., Ung, C.-H., Guindon, L., Piercey, D.E., Lambert, M.-C. & Beaudoin, A. 2002. A strategy for mapping Canada's Forest biomass with Landsat TM imagery. IEEE 3: 1312–1315.

Madgwick, H.A.I. 1982. Forest Biomass. Kluwer Academic Publishers. 164 p.

Marklund, L.G. 1987. Biomass Functions for Norway Spruce (*Picea abies* (L.) Karst.) in Sweden. Sverig Lantbruksuniversitet, Institutionen för skogstaxering. Rapport 43 pp. 1–127.

— 1988. Biomassafunctioner for Tall, Gran Och Björk i Sverige. Sverig Lantbruksuniversitet, Institutionen för skogstaxering. Rapport 45. p. 1–73.

Muukkonen, P. & Mäkipää, R. 2006. Biomass equations for European trees: addendum. Silva Fennica 40: 763–773.

—, 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: 231–245.

— 2007. Generalized allometric volume and biomass equations for some tree species in Europe. European Journal of Forest Research 126: 157–166.
Mälkonen, E. 1974. Annual primary productivity and nutrient cycle in some pine stands. Communications Instituti Forestalis Fenniae 84.5.
Niklas, K.J. 1994. Plant Allometry. The Scaling of Form and Process. The University of Chicago Press, Chicago.
Næset, E. 2002. Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. Rem. Sens. of Env. 80: 88–99.
Ovington, J.D., Forrest, W.G. & Armstrong, J.S. 1967. Tree biomass estimation. Symposium on primary productivity and mineral cycling in natural ecosystems. American Association for the Advancement of Science, 13th Annual Meeting, New York City, December 27, 1967. University of Maine Press, Orono.
Paavilainen, E. 1980. Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. Communicationes Instituti Forestalis Fenniae No. 98–5.
Pajtíka, J., Konôpkaa, B. & Lukac, M. 2008. Biomass functions and expansion factors in young Norway spruce (*Picea abies* [L.] Karst) trees. For. Ecol. Manage. 256: 1096–1103.
Pare, D. & Bergeron, Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. The Journal of Ecology 83: 1001–1007.
Parresol, B.R. 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. For. Sci. 45: 573– 593..
Persson, H.Å. 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil 71: 87–101.
Petersson, H. & Stähl, G. 2006. Functions for below-ground biomass of *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Betula pubescens* in Sweden. Scand. J. For. Res. 21: 84–93.
Pietikäinen, J., Vaijärvi, E., Ilvesniemi, H., Fritze, H. & Westman, C.J. 1999. Carbon storage of microbes and roots and the flux of CO_2 across a moisture gradient. Can. J. For. Res. 29: 1197–1203.
Rana, B.S., Singh, S.P., & Singh, R.P. 1988. Biomass and productivity of Chir pine (*Pinus rosburghil* Sarg.) forest in central Himalaya. Proc. Indian Sci. Acad. B54: 71–74.
Rawat, Y.S. & Singh, J.S. 1988. Structure and function of oak forests in central Himalaya. I. Dry matter dynamics. Annals of Botany 62: 397–411.
Reich, P. B. & Oleksyn, J. 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. Ecology Letters 11: 588–597.
Repola, J. 2006. Models for vertical wood density of Scots pine, Norway spruce and birch stems, and their application to determine average wood density. Silva Fennica 40: 673–685.
—, Ojansuu, R. & Kukkola, M. 2007. Biomass functions for Scots pine, Norway spruce and birch in Finland. Working Papers of the Finnish Forest Research Institute 53, Finland.
— 2008. Biomass equations for birch in Finland. Silva Fennica 42: 605–624.
Rignot, E., Way, J., Williams, C. & Viereck, L. 1994. Radar estimates of aboveground biomass in boreal forests of interior Alaska. IEEE Transactions on Geoscience and Remoter Sensing 32: 1117–1124.
Rouvinen, S., Rautiainen, A. & Kouki, J. 2005. A relation between historical forest use and current dead woody material in a boreal protected old-growth forest in Finland. Silva Fennica 39: 21–36.
Sarvas, R. 1964. Havupuut [Conifers]. Werner Söderström Osakeyhtiö, Porvoo Helsinki.

510 p.
Satoo, T. 1982. Forest Biomass. Dr. W. Junk Publisher, The Hague. 164 p.
Schweingruber, F.H. 1996. Tree Rings and Environment Dendroecology. Paul Haupt Publishers, Berne. 609 p.
Scotter, G.W. 1963. Productivity of arboreal lichens and their possible importance to barren-ground caribou (*Rangifer arcticus*). Archivum Societatis Zoologicae-Botanicae Fennicae Vanamo 16: 155–161.
— 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. Wildlife Management Bulletin, Ottawa, Series 1, 18: 1–111.
Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964. A quantitative analysis of plant form: the pipe model theory. I. Basic analyses. Jpn. J. Ecol. 14:133–139.
Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., III, F.S.C. & Jr., P.W.S. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change 56: 274–296.
Somogyi, Z., Cienciala, E., Mäkipää, R., Lehtonen, A., Muukkonen, P. & Weiss, P. 2007. Indirect methods of large-scale forest biomass estimation. European Journal of Forest Research 126: 197–207.
Sprugel, D.G. 1984. Density, biomass, productivity, and nutrient-cycling changes during stand development in wave-regenerated balsam fir forests. Ecological Monographs 54: 165–186.
Tackenberg, O. 2007. A New Method for Non-destructive Measurement of Biomass, Growth Rates, Vertical Biomass Distribution and Dry Matter Content Based on Digital Image Analysis. Annals of Botany 99: 777–783.
Trass, H. (1965) Lishaynikovye sinuzii kak komponent biogeotzenozov (ekosistem). In Problemy izucheniya gribov i lishaynikov. –IV Simpozium Pribaltiyskikh Mikologov i likhenologov, Tartu [abstracts]: 207–211. Tartu: Akademiya Nauk Estonskoy SSR.
Valentine, H.T., Baldwin, V.C., Gregoire Jr., T.G. & Burkhart H.E. 1994. Surrogates for foliar dry matter in loblolly pine. For. Sci. 40: 576–585.
Waring, R.H. & Franklin, J.F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204: 1380–1386.
Whittaker, R.H., Woodwell, G.M. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. J. Ecol. 56: 1–25.
Zheng, D., Heath, L.S. & Ducey, M.J. 2007. Forest biomass estimated from MODIS and FIA data in the Lake States: MN, WI and MI, USA. Forestry 80: 265–278.
Zianis, D., Muukkonen, P., Mäkipää, R. & Mencuccini, M. 2005. Biomass and stem volume equations for tree species in Europe. Silva Fennica Monographs 4. 63 p.
Zhai, M. 1982. Biomass and nutrient cycling studies in some mixed stands of pine and maple in Xishan area, Beijing. Journal of Beijing Forestry University (4): 67–79 (in Chinese).

APPENDIX

Appendix 1 Tree biomass data set for Scots pine and Norway spruce forests in the vicinity of southern Finland (58.00-62.13 ^{o}N, 14–34 ^{o}E, ≤ 300 m a.s.l.) compiled based on Cannell (1982).

Species	Country	Latit (°)	Longit (°)	Altit (m)	MAT (°C)	APP (mm)	Age (yr)	TTB (Mg ha^{-1})	AGB (Mg ha^{-1})	Sources
Pinus sylvestris	Sweden	62.10	14.50	295			84	144.4	127.5	Albrektson 1980
Picea abies	Former USSR	62.00	34.00	140	2.2	650	22	32.1	25.9	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	37	76.1	62	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	45	94	78.2	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	54	119.7	98.1	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	41	51.2	41.7	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	42	42.5	34.5	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	43	97.3	80.5	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	38	105.7	87.4	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	37	34.9	28.3	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	39	84.2	69.6	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	45	56	45.9	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	68	161.8	132.7	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	82	177.7	144.5	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	98	226.6	185.6	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	109	237.7	192.7	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	126	255.1	209.1	Kazimirov & Morozova 1973
Picea abies	Former USSR	62.00	34.00	140	2.2	650	138	248.4	200.9	Kazimirov & Morozova 1973

Continued Appendix 1

Species	Country	Latit (°)	Longit (°)	Altit (m)	MAT (°C)	APP (mm)	Age (yr)	TTB (Mg ha^{-1})	AGB (Mg ha^{-1})	Sources
Picea abies	Finland	61.67	24.32	140	2.9	576	47	52.95	41.94	Mälkönen 1974
Picea abies	Sweden	60.55	14.25	300			145	107.3	83.8	Albrektson 1980
Pinus sylvestris	Sweden	60.55	14.05	300			145	103.7	83.1	Albrektson 1980
Pinus sylvestris	Sweden	60.52	16.25	185-205			28	105.3	93.1	Albrektson 1980
Pinus sylvestris	Sweden	60.52	16.25	185-205			29	90.6	81.5	Albrektson 1980
Pinus sylvestris	Sweden	60.52	16.25	185-205			34	94.8	81.1	Albrektson 1980
Pinus sylvestris	Sweden	60.52	16.25	185-205			50	88	75.9	Albrektson 1980
Pinus sylvestris	Sweden	60.52	16.25	185-205			77	90.8	79.4	Albrektson 1980
Pinus sylvestris	Sweden	60.52	16.25	185-205			100	113.3	94.3	Albrektson 1980
Picea abies	Finland	60.52	23.88	135	3.7	545	28	24.98	17.94	Mälkönen 1974
Picea abies	Finland	60.52	23.85	125	3.7	545	45	95.2	75.92	Mälkönen 1974
Pinus sylvestris	Sweden	60.48	16.25	170-205			9	30.1	27.6	Albrektson 1980
Pinus sylvestris	Sweden	60.48	16.25	170-205			12	15.6	14.2	Albrektson 1980
Pinus sylvestris	Sweden	60.48	16.25	170-205			14	35.6	32.1	Albrektson 1980
Pinus sylvestris	Sweden	60.48	16.25	170-205			14	30.8	28	Albrektson 1980
Pinus sylvestris	Sweden	60.48	16.25	170-205			26	116.2	105.3	Albrektson 1980
Pinus sylvestris	Sweden	60.48	16.25	170-205			27	98.2	88.1	Albrektson 1980
Pinus sylvestris	Sweden	60.20	17.13	10			13		18.1	Albrektson 1980
Pinus sylvestris	Sweden	60.20	17.13	10			13		34	Albrektson 1980
Pinus sylvestris	Sweden	60.20	17.13	10			13		31.1	Albrektson 1980
Pinus sylvestris	Sweden	60.20	17.13	10			13		26.2	Albrektson 1980
Pinus sylvestris	Sweden	60.20	17.13	10			13		28.2	Albrektson 1980

Continued Appendix 1

Species	Country	Latit (°)	Longit (°)	Altit (m)	MAT (℃)	APP (mm)	Age (yr)	TTB (Mg ha-1)	AGB (Mg ha-1)	Sources
Picea abies	Former USSR	58.00	27.50		4.7	568	84	238	173.4	Kolli 1970
Picea abies	Former USSR	58.00	27.50		4.7	568	51	187.9	142.1	Kolli 1970
Pinus sylvestris	Finland	60.78	30.96	145	1.9	649	15	14.9	11.1	Helmisaari et al. 2002
Pinus sylvestris		60.78	30.96	145	1.9	649	35	53.5	42.2	Helmisaari et al. 2002
Pinus sylvestris		60.78	30.96	145	1.9	649	100	139.7	121.3	Helmisaari et al. 2002