Evaluation of performance of tree-level biomass models for forestry modeling and analyses

Leena Kärkkäinen

METSÄNTUTKIMUSLAITOS

Jalostusosasto

Evaluation of performance of tree-level biomass models for forestry modeling and analyses

Leena Kärkkäinen

Academic Dissertation

To be presented, with the permission of the Faculty of Forestry of the University of Joensuu, for public criticism in Auditorium Käpy of the Finnish Forest Research Institute, Yliopistokatu 6, Joensuu, on 7th May 2005, at 12 o'clock noon.

Joensuu 2005

**Author's contact
information**   **Adress:** Leena Kärkkäinen, Finnish Forest Research
                         Institute, Joensuu Research Centre
                         P.O. Box 68
                         FIN-80101 JOENSUU, FINLAND
                         Tel: +358 10 211 3044
                         Fax: +358 10 211 3113
                         E-mail: Leena.Karkkainen@metla.fi

Abstract

In forestry modeling and analyses, the evaluation of the performance of the models is needed in order to analyze the applicability of the models as a part of a large modeling system. In previous studies, no systematic and detailed analyses of available biomass models to evaluate their applicability for the determination of carbon sequestered by trees and for the assessment of energy wood resources in a certain area were usually made. The aim of this study was to analyze the performance of available biomass models for estimation of biomass of trees in forestry modeling and analyses. This study was the first attempt to systematize the evaluation of the set of biomass models describing the different components of a tree. A set of Marklund's (1988) and Hakkila's (1972a, 1979, 1991) models were selected from the available biomass models for the estimation of the total biomass and its distribution into different components of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birches (*Betula pendula*, *B. pubescens*) growing on different sites throughout Finland.

Typically, the models are evaluated using statistical analyses. However, the statistical tests do not provide information about the performance of the models outside the testing data. In this study, due to the lack of representative empirical data, the biomass models were evaluated using other methods than statistical tests. Available models for the estimation of biomass at tree level were mapped using literature. The representativeness of the biomass models was evaluated by studying the structure of modeling data, capability of the models to describe different components of a tree and capability of used independent variables to describe the biomass of different components of a tree. The outputs of the selected Marklund's (1988) and Hakkila's (1972a, 1979, 1991) models were evaluated in relation to each other and compared with other studies. The comparisons were made on mineral soils and on peatlands, on fertile and on infertile mineral soils and in Southern, and in Northern Finland both. Furthermore, in a case study, the models were incorporated into the MELA forest planning system, and the applicability of the models for the large-scale calculations was analyzed. In the analyses, optimization was utilized to point out differences between the outputs calculated using different sets of models.

Marklund's (1988) models proved to be more applicable than Hakkila's (1972a, 1979, 1991) models for the estimation of biomass of different components of trees. The data behind Marklund's (1988) models were the most representative compared to other models available for biomass calculations at tree level. Although the data were collected from Sweden, the variability in the data covers well the variability of the site conditions and structure of tree populations in Finland, too. Despite the wider range of growing conditions included into Marklund's (1988) data, based on comparisons between the outputs of Marklund's (1988) and Hakkila's (1972a, 1979, 1991) models, Marklund's (1988) models are also applicable in Finland. The models for different biomass components are derived from the same sample trees of pine and spruce for most of the components except the finest fraction of roots. Furthermore, Marklund (1988) has formulated models for different components of birch excluding stump, roots and leaves. In addition, from Marklund's (1988) mod-

els for the biomass of above-ground components of pine and spruce it was possible to get full sets having both breast height diameter and height as independent variables. Excluding the living branches, Marklund (1988) had also models having both breast height diameter and height for the modeled above-ground components of birch. Marklund's (1988) models provided acceptable estimates for the biomass of different components of trees over the whole diameter range irrespective of the tree species.

When the total above-ground biomass of trees is considered, Marklund's (1988) models produce logical estimates throughout Finland. The models are at their best in regularly managed stands dominated by Scots pine. With regard to single components of a tree, the biomass models are the most applicable for the estimation of the biomass of the stem wood and that of stem bark. The uncertainty concerning the outputs of the models increases, when the deviation of the structure of the data used for the estimation of biomass of trees from the original modeling data increases. Based on this study, the performance of the models in terms of the biomass of stem wood and stem bark is realistic as regards the location and the fertility of site, but much more uncertainty is involved in the estimation of biomass of other components of a tree. All these results about the performance of Marklund's (1988) models must also be taken into account, when the outputs of the models are used as a goal or a constraint in the optimization.

Based on the analyses made in this study, Marklund's (1988) models are more applicable for the estimation of carbon sequestration of the above-ground components of trees than for the estimation of energy wood resources. Most of the above-ground components of trees consists of stem wood, for which Marklund's (1988) models produced realistic outputs. The energy wood consists mostly of living branches, and the biomass estimates of the models for living branches were more unreliable.

As a conclusion, the evaluation of the models made in this study facilitated the determination of the model structure. Furthermore, it was possible to identify the special feature of the model performance, with an increase in understanding how the set of biomass models were functioning at different level of applicability (tree, stand, forest area). The evaluation produced information about the realism and generality of the model outputs, but the study of accuracy would have demanded empirical data. The lack of knowledge could be identified in order to direct the future studies to fill the gaps in the knowledge. Also the uncertainties in the model calculations could be identified.

In this study, the methods were represented for the systematization of the evaluation of the set of biomass models for different components of a tree. The evaluation of the set of models for different components of a tree demanded a versatile study of the models in relation to each other. The methods used in this study were based on more efficient utilization of existing data and research results than usually have been made in the evaluation of the models. Although the statistical tests would not be possible for the evaluation of the models, this study showed that useful information about the performance of the models could be obtained using other evaluation methods.

Acknowledgements

CONTENTS

DEFINITIONS

Above-ground components of a tree	Components of a tree above the stump level.
Basic density	Relation between dry mass and green volume (kg/m^3).
Biomass	Mass of organic matter (kg). In this study biomass refers to dry mass of wood and bark (if not otherwise specified).
Calculation period	The time period for which the analyses were made in the MELA forest planning system. In this study the calculation period of 50 years was divided into five sub-periods of 10-years.
Dry mass	Mass of dried organic matter (kg).
Green mass	Mass of both water and dry matter, which organic matter includes (kg).
Sub-period	The period for which the variables are estimated in the MELA forest planning system. In this study five sub-periods of 10-years were used.
Tapering	The difference between the diameter at breast height (1.3 m) of a stem and the diameter at a height of 6 m (cm).

SYMBOLS

$\alpha, \beta, \gamma, \delta, \zeta, \eta, \theta$	Parameters
ε	Error term
BEF	Biomass expansion factor: a multiplier used to convert stem volume into the biomass of different components of a tree
CO_2	Carbon dioxide
cr	Crown ratio: relation between the length of living crown and the tree height
CT	Dummy variable. CT = 1, if a tree grows on dry forest sites (*Calluna* sites according to forest type classification used in Finland), otherwise CT = 0
d	Diameter at breast height (1.3 m) (cm, if not otherwise specified)
d.d.	Degree days
FFRI	Finnish Forest Research Institute
h	Height (m, if not otherwise specified)
h_{rel}	Relative height of a tree, the height of a tree in relation to the dominant height of trees
IR	Ombrotrophic bog
k	Correction term for knots and bark
l_c	Length of living crown (m)
l_{cl}	The height of crown limit, the distance between ground level and the lowest living branch (m)
m	Dry mass (kg, if not otherwise specified)
MK	*Vaccinium myrtillus* spruce mire

m_{t1}	Biomass of living trees in the time t1 (Mg)
m_{t2}	Biomass of living trees in the time t2 (Mg)
n	Number of sample trees
NC	Net carbon sequestered by trees (Mg)
NFI	National forest inventory
NPV	Net present value (€)
R	Multiple correlation coefficient
R^2	Coefficient of determination
RhNRmu	Herb-rich sedge pine mire
s	Standard deviation (cm, m)
s_{res}	Residual standard deviation (kg or ln(kg))
t	Age at breast height (years)
t_b	Biological age (years)
V	Stem volume with bark (m^3)
V_{bl}	Stem volume without bark (m^3)
VNRmu	Ordinary sedge pine mire
V_o	Stem volume with or without bark (m^3)
$\overline{x}$	Mean value (cm or m)

1 INTRODUCTION

1.1 Need for biomass estimation of trees in forestry modeling and analyses

Forests play an important role in fixing atmospheric carbon dioxide (CO_2) (e.g. Hoen and Solberg 1994, Marttila et al. 2000, Sedjo 2000). In Finland, the extent of carbon sink of trees has been estimated to correspond to half of the CO_2 emissions of fossil fuels (Forsius et al. 1996). The carbon sink of trees can be increased and thus the emissions of CO_2 to the atmosphere can be slowed down by protecting and increasing the area of forests and the volume of growing stock (Mikkelä et al. 2000). The emissions of CO_2 can also be slowed down by replacing non-renewable energy resources with wood and other renewable biomass (Mikkelä et al. 2000). In Finland, the proportion of wood-based energy resources is ca. 20% of the total energy consumption (Finnish Statistical Yearbook of Forestry 2003).

For the determination of carbon sequestered by trees and for the assessment of energy wood resources the biomass estimations of trees are needed. The carbon sequestered by a tree is usually expressed as a certain fraction of biomass of a tree (Karjalainen et al. 1994, Nurmi 1997). The amount of different components of crown, stumps and roots can be estimated most practically by using mass as a measure (Hakkila 1989). The biomass can be expressed as green mass or dry mass. Green mass is the mass of water and dry matter, and dry mass merely the mass of dry matter. Usually the dry mass is determined by drying green mass samples at 105°C (e.g. Marklund 1987, Finér 1991). The dry mass is a more useful measurement of biomass than green mass, because the water content of trees can vary considerably. In this study biomass refers to the dry mass, if it is not otherwise specified.

The amount of carbon sequestered by trees and the biomass of trees should be taken into account in also in forestry modeling and analyses. The period of time to maintain a high growth rate (Schroeder and Ladd 1991), the allocation of growth to different components of a tree (Oliver 1992) and the ability to store carbon (Schroeder and Ladd 1991, Dixon et al. 1994) vary between tree species. Therefore, the decisions concerning the selection of tree species have effects on the carbon sequestration of trees and the amount of energy wood resources. In addition, the carbon sequestered by trees and the amount of tree biomass in stands as a whole can also be affected e.g. by regulating the rotation length of tree stand (Sedjo 2000, Liski et al. 2001, Ericsson 2003) and the intensity and frequency of thinnings or by ditching and fertilizing (Castrén and Simula 2000).

In Finland information about carbon sequestration of trees at the national level is currently collected as part of forestry statistics (Finnish Statistical Yearbook of Forestry 2003). The carbon balance of forests is taken as an indicator of the sustainability of forestry in Finland (Mikkelä et al. 2000). In addition, the carbon sequestration of trees has already been taken into account in the formulation of national (Maa- ja metsätalousministeriö 1999) and regional forest programs (e.g. Lounais-Suomen metsäkeskus 2001). Furthermore, information on carbon flows of

forest sector is required for the determination of national level climate policy (Sievänen 2000).

In the future, the carbon flows of trees should be included in the environmental impact assessment related to all planning and decision-making processes. The selling of the spare capacity of carbon sequestration may be an alternative to the selling of timber (Hildén et al. 1999). In the future, also the information about energy wood resources and the use of logging residues for energy needs can be documented in national forestry statistics. The information about the amount of logging residues can also be used in order to determine the available material for energy production – e.g. for a single power plant (Asikainen et al. 2001) or for a single household. In addition, biomass estimates are needed in the evaluation of the environmental impacts (e.g. nutrient losses) of harvesting the logging residues for energy wood.

1.2 Estimation of biomass using stand- and tree-level models

In Finland the estimates on the carbon sequestration of growing stock and on the energy wood resources have been commonly made using stand-level models. The estimates have usually been based on average characteristics of trees in a certain region (e.g. Mattila and Keskimölö 1994, Hakkila et al. 1995, Kauppi et al. 1995, Vesterlin 1996, Sirén et al. 2000, Asikainen et al. 2001, Lounais-Suomen metsäkeskus 2001, Finnish Statistical Yearbook of Forestry 2003). For example, at the national level the carbon balance of tree stands during a certain period has been calculated on the basis of national forest inventory (NFI) data as a difference between the total amount of carbon of growth and that of removal. The species-specific conversion factors (Karjalainen and Kellomäki 1996) have been used to convert the volume of stem growth and that of removal to the biomass and carbon corresponding the growth and removal of all components of trees (Marttila et al. 2000). Recently, Lehtonen et al. (2004) developed biomass expansion factors (BEFs) for the estimation of carbon stock. These BEFs were dependent on stand age and dominant tree species. In order to formulate BEFs, the biomass of a component and the stem volume were estimated for each tree using tree-level models. Thereafter, at stand level the BEFs were estimated as a relation between the sum of dry mass of a tree component and that of stem volume. Finally, the age-dependent BEF for a component was estimated as a function of stand age using linear regression.

The stand-level models, which are based on the BEFs (or other conversion factors) are useful where the data includes stem volume estimates (Losi et al. 2003) and only very coarse biomass estimates are needed. A problem in the use of BEFs is that they describe only trees growing in certain stand structures. The variation of a tree biomass between different stands and inside a single stand cannot be described properly by using BEFs. In order to take into account the biomass of trees in various growing conditions, the great number of BEFs would be needed, and therefore their use would become complicated. A problem in the formulation of BEFs is, that the stem volume and biomass functions should be derived from the

same data and the formulas of the functions should be compatible. The use of stem volume functions derived from different data than biomass functions can cause compatibility problems between the models, which can have effects on the values of BEFs. The estimation of uncertainties is also difficult if the volume and biomass models represents different populations and if the models cannot be tested quantitatively in the population in which they are applied.

In addition to stand-level models, energy wood resources have been predicted using tree-level models in Finnish studies (e.g. Hynynen 2001, Malinen et al. 2001). In these studies the biomass was estimated for sample trees describing the size distribution of trees growing in a forest area. The estimation of biomass of trees using tree-level models has many advantages compared to the estimation of biomass of trees based on stand-level or forest area level models. When the tree-level models are used, the structure of forests can be described in more detail. The tree-level models take into account competitive interactions within a stand (Chertov et al. 1999, Porté and Bartelink 2002). Therefore, the effects of stand density, species mixture (Knowe et al. 1997, Hasenauer 2001), various size classes (Knowe et al. 1997) and age (Hasenauer 2001) can be taken into account using the tree-level models. Also the effect of site fertility and site location on the form of a stem and a crown, and thus on the amount of energy wood resources and carbon sequestered by trees can be taken into account by using tree-level models. The effects of forest management on the growth of trees (Siitonen 1996, Hasenauer 2001, Nuutinen and Kellomäki 2001) and on the amount of different timber assortments can be determined more accurately using tree-level models than using stand-level models. The main problem in using tree-level models is that tree-level data is not always available, and thus, the size distributions of trees in a stand must be regenerated based on stand-level variables using theoretical distributions. This causes extra work and adds uncertainty to the biomass estimates.

The biomass of an individual tree can be estimated using weight tables (e.g. Hakkila et al. 1978, Baskerville 1965), expansion factors (e.g. Field measurement... 2002) or regression functions (e.g. Parresol 1999). In the simplest species-specific weight tables, the biomass of different components of a tree can be determined according to diameter at breast height (Baskerville 1965). In addition to tree species and diameter at breast height, tree height and taper class are used for the estimation of stem biomass in the weight tables (e.g. Hakkila 1979). The main limitation for the use of weight tables is the difficulty of the use of multidimensional tables.

At tree level, expansion factors are used to convert the stem volume into aboveground biomass of a tree and into the biomass of different components of a tree (Harkin and Bull 2000, Field measurement... 2002). These expansion factors are, however, average estimates for a tree species, and thus, they do not take into account the characteristics of an individual tree. Therefore, the biomass estimates calculated for trees in a stand using tree-level expansion factors have the same limitations as those produced using stand-level expansion factors.

Tree biomass may also be estimated using regression functions. The regression functions usually predict directly the dry mass of a component of a tree (e.g. Finér 1989, Korhonen and Maltamo 1990, Finér 1991, Hakkila 1991, Laiho 1997). However, the dry mass of a stem is sometimes estimated by multiplying the average

basic density of a stem calculated using regression function with the green volume (e.g. Hakkila 1979, Bergstedt and Olesen 2000, Stakanov et al. 1998). In allometric regression functions the mass of a component is related to one or more dimensions of the standing tree (e.g. Parresol 1999, Field measurement... 2002). The tree characteristics related to the amount of biomass and usually determined in forest inventories are tree species, diameter at breast height, height, diameter increment, height increment, age at breast height, and crown limit. In forest inventories the stand conditions are often described using stand density, stratum, site fertility and site location. All these stand characteristics have effects on the allocation of biomass. Of these variables, diameter at breast height, height, age and crown limit are commonly used for the biomass functions (e.g. Hakkila 1970, 1971, Hakkila et al. 1978, Simola 1977, Mälkönen and Saarsalmi 1982, Björklund 1984, Marklund 1988, Finér 1989, Saarsalmi and Mälkönen 1989, Finér 1991, Hakkila 1991, Laiho 1997).

The use of the regression functions is common because they can easily be applied using computers (Hakkila 1989). The regression functions require only a few steps to estimate biomass once a regression has been prepared (Losi et al. 2003). The estimation of uncertainties is easier than that of expansions factors, for example. A problem concerning the use of regression functions can be that suitable variables are not available in the data.

1.3 Incorporation of tree-level biomass models into the forestry modeling and analyses

In Scandinavia, tree-level biomass models have been implemented in some forest planning systems. In Norway, the CO_2 fixation of trees has been modeled in a long-range forest management planning model, called GAYA-LP, by a sub-model, which is based on Marklund's (1988) biomass models and a conversion factor, which was used in order to calculate the amount of fixed CO_2. By using this sub-model the potential for increasing the net carbon sequestration related to timber production by changes in the forest management over a time period of 30 years was studied (Hoen and Solberg 1994). In Sweden, the Hugin model was used to study the effects of rotation length on the carbon accumulation in biomass and soil and the amount of harvest residues that could substitute for fossil fuel. Marklund's (1988) biomass functions were used in the Hugin model to calculate the dry mass of different components of trees (Ericsson 2003).

In Finland, the MELA forest planning system (Siitonen et al. 1996, Redsven et al. 2004) is commonly used for estimating the production potentials of forests and for solving the optimal management of forest stands according to specific goals and constraints (Siitonen 1993). It consists of an automated stand simulator based on individual trees and the optimization package based on linear programming, JLP (Lappi 1992). Mielikäinen et al. (1995), Malinen and Pesonen (1996) and Malinen et al. (2001) used undocumented tree-level models with the MELA system to estimate the fuel wood potential based on different cutting scenarios. Minkkinen et al.

(2001) used MELA with Marklund's (1988) models in order to study tree stand development and carbon sequestration on drained peatland stands in Finland.

Specific demands are set for the biomass models that are incorporated into forestry modeling and analyses. These demands depend on the objective of a user and the purpose of the forest planning system used as a tool for the analyses. Typically, forest planning systems are used to generate estimates on the current and future forest resources on large forest areas.

The first demand is that the models incorporated into the forestry modeling and analyses have to be widely applicable. The biomass models should be able to describe the biomass of different tree species and the whole size range of trees. They should cover the trees growing in different stories, different stand densities, different sites and different parts of the country.

The second demand is that the biomass estimates must be provided for all components of a tree. If many different divisions of biomass components are needed, they must be compatible with each other and with other models used in forestry modeling and analyses. The functions should be derived for each component of a tree from the variables describing the same sample trees. The combination of the models from separate studies may cause the distortion in the relation of components of a tree. In addition to differences in modeling data, there may be variation in the definition of a component in different studies. If the biomass of a whole tree is estimated using a separate function, the sum of different biomass components should correspond to that function (Parresol 1999). However, in many studies equations for total above-ground biomass have not been formulated, and thus, the attempts to estimate total biomass by addition of estimates of the components might be biased. For example, when the biomass of components are estimated using log-transformed allometric relationships, the sum of the component biomass is not the same as when the total biomass is estimated directly by an allometric relationship (Snowdon et al. 2002).

Parresol (1999) represented three procedures for forcing additivity of a set of linear tree biomass functions. In procedure 1, the total biomass regression function is defined as the sum of the separately calculated best regression functions of the biomass of its components. In procedure 2, the same independent variables are used in the least squares linear regressions of the biomass of each component and that of the total, and thus, the additivity of the components is ensured. In procedure 3, the generalized least squares regression with dummy variables techniques is used. The total-tree regression is a function of all independent variables used in the regression for each component of a tree. The additivity of the functions is ensured by setting constraints on the regression coefficients. Parresol (2001) demonstrated two procedures for forcing additivity of a set of nonlinear models. Procedure 1 is the same as the procedure 1 in the case of linear functions. In procedure 2, nonlinear joint-generalized least squares regression is used. Otherwise the procedure is the same as in procedure 3 in the context of linear functions.

In forestry modeling and analyses, it is not usually enough to estimate just the biomass of standing trees. Thus, the second demand concerns also the biomass estimates of different components of cut trees. For the determination of the biomass of different timber assortments, it is necessary to allocate the biomass of the stem between the different assortments. In energy wood harvesting, some parts of

the branches and needles – and even some parts of stumps and roots – are taken away from the forest. Therefore, it is also necessary to evaluate the biomass of these components. There is a need for models that can provide the information about the changes vertical distribution of the biomass of the different tree components in lengthwise direction of the tree can be achieved. There is also an increasing demand for modeling the biomass of dead trees. The mass loss of dead trees over time must be taken into account. It should also be noted that different definitions of the components should be applied for dead trees than for living trees.

The third demand is that the independent variables used in biomass models should be measured in forest inventories, or should be able to be estimated from forest inventory data easily and reliably. The use of independent variables in a biomass model for a certain component of a tree must be compatible with that for other components of a tree. In principle, the most accurate estimates of biomass of a component of a tree in relation to other components can be achieved, if the same independent variables are used for the modeling of all components. The exclusion of an independent variable simplifies the model, but causes error in the relation of the outputs of the models formulated for the different components of a tree.

1.4 Model evaluation methods

Before the use of the models the adequacy of the models for the intended purpose and context must be assessed. Typically, the outputs of the models are tested only against the empirical testing data. However, this kind of testing does not usually cover all situations in which the models are intended to be used. Furthermore, in many cases the testing of outputs of models is impossible due to lack of empirical data. Thus, when the data are lacking, the analysis of the applicability of the models for a certain purpose has not usually been made or it has been inadequate. For example, in the previous studies (e.g. Hoen and Solberg 1994, Mielikäinen et al. 1995), no systematic and detailed analysis was carried out of existing tree-level biomass models to evaluate their applicability in the assessment of carbon stock of trees and energy wood resources in a certain area.

In the literature, evaluation of the models has commonly been referred to using such terms as *verification* and *validation* (e.g. Caswell 1976, Mayer and Butler 1993, Power 1993, Rykiel 1996, Prisley and Mortimer 2004). For example Rykiel (1996) has defined verification as a demonstration that the modeling formalism is correct, and validation as a demonstration that a model meets some specified performance standards under specified conditions. However, some authors (e.g. Cale et al. 1983, Soares et al. 1995, Vanclay and Skovsgaard 1997) have recommended that the terms *verification* and *validation* should be avoided because of the semantic and philosophical controversies associated with them (e.g. Oreskes et. al. 1994, Soares et al. 1995). Therefore, in this study the general term *evaluation* was used to cover the acceptability analysis of the models for a certain use (compare Soares et al. 1995, Vanclay and Skovsgaard 1997).

The evaluation should provide information about the behavior and predictive ability of the model (Soares et al. 1995, Vanclay and Skovsgaard 1997). It is not

possible to prove the absolute correctness of a model (e.g. Oderwald and Hans 1993). However, the credibility of a model, and thus, the user's confidence about the adequacy of the model for its intended uses, increases with the rigor of the tests the model passes (e.g. Caswell 1976, Oderwald and Hans 1993, Power 1993, Vanclay and Skovsgaard 1997). The analysis of models may also indicate where the knowledge is lacking (Mankin et al. 1979) and where future data collection and model revision efforts may be most useful (Soares et al. 1995, Vanclay and Skovsgaard 1997).

Evaluation procedure should include quantitative and qualitative examinations of model performance. The aim of qualitative evaluation is to ensure that the model and its components are necessary, are biologically realistic, agree with existing theories, and provide sensible responses to management actions (Soares et al. 1995). In many previous studies only quantitative evaluation of the models has been made. The quantitative evaluation informs about accuracy of the model (Robinson and Ek 2000), but does not guarantee that the scientific basis of the model and its internal structure correspond to actual processes or cause–effect relationships operating in the real system (Rykiel 1996). It comprises commonly statistical tests and comparisons of predictions with empirical data that are independent of the data used to fit the model (Soares et al.1995) and belong to the population to which the models are to be applied (Robinson and Ek 2000). In addition, the quantitative evaluation should comprise, for example, the determination of limits for the use of a model on the basis of model form.

In some cases, the quantitative evaluation of the models using statistical tests is impossible due to lack of representative data. Thus, the model must be examined at least for reasonableness and completeness without reference to empirical data (Mankin et al. 1979). The evaluation of the models should include at least the study of the applicability of the models for trees having different sizes and growing in different conditions. In the evaluation of different models one of the main interests is, how well a model performs in relation to other models (Buchman and Shifley 1983). Thus, the comparison of the output of one model to that of another model, if comparable models exist, is an important evaluation method.

The study of modeling data reveals preliminary information about the range of applicability of the models. The structure of data used for the formulation of the models should correspond to the one for which the models are used. In practice, this requirement is difficult to meet. Therefore, attention should be paid to the evaluation of the influence of the modeling material to the results and to the estimation of biases of the outputs of the models in the application areas where the models are used. The evaluation should also take into account that the structure of forests will change over time; this also applies to the areas from which the models are derived. In many cases extrapolation is needed, and it adds much uncertainty to the results. However, according to some studies (e.g. Keller et al. 2001) it may be the most cost-effective to resolve uncertainties for the most common diameter classes, because the improvement of the certainty of, for example, very large trees might result only in small improvements in total estimates. If all sizes of trees and site conditions are not included to the modeling material, at least the behavior of the model outside the range of data should be carefully checked and the restrictions to the use of models should be clearly determined.

Also the study of independent variables gives useful information about the performance of the model. The need for and the effect of different independent variables have to be analyzed. A model including many independent variables is more flexible and can better describe the variation of dependent variables (Ranta et al. 1997). However, the aim of regression analyses is to find out the best independent variables, and thus, if the independent variables are strongly correlated with each other, not all of them should be included into the model, because they explain the same phenomenon (Ranta et al. 1997). The analysis of the effect of an independent variable should include the study of positive or negative effects, the effect of transformation, and the magnitude of the effect on the biomass.

The more detailed evaluation of the models is the comparison of output of one model to that of another model. Models to be compared should be independent and based on different underlying principles (Rastetter 1996). The inventory data are needed to derive the real relationships between the different independent variables used in the models. The outputs of the models must be compared also outside the range of modeling data. Also the models, which are mathematically very different may be virtually indistinguishable in terms of their fit to the data, but may give very different predictions outside the range of the data (Chatfield 1995).

The comparison of the models reveals what kind of outputs the models produce in relation to each other. Thus, if the outputs disagree, then neither of the models can be falsified (Rastetter 1996). If all available models give similar results, models can be considered to be structurally reasonable (Kangas 2001a). If different models produce parallel results, the comparisons of the outputs of the models give useful information about the magnitudes of the studied variable in trees of different sizes. By comparing the outputs of the models on different sites and in different geographical regions it is possible to get some kind of guidelines about the variability of the studied variable along the site fertility and geographical location, if the models produce similar results.

Although the available models may produce similar outputs, there is however, a possibility that the models are based on the same faulty assumptions, and therefore, several poor models may make similar predictions (Leary 1997, Kangas 2001a). The realism of the models has to be studied by comparing the model outputs with broad expectations derived from ecological or physiological knowledge (see Robinson and Ek 2000). If the similar outputs of the compared models also correspond to the previous knowledge, the selection between the models may be based on extra-evidential considerations, such as symmetry, simplicity and personal preferences (Oreskes et al. 1994).

When the models are incorporated into a forest planning system, the evaluation of the models as a part of such a system is required. In a forest planning system the models must produce reasonable results in relation to other models, and thus, the outputs of incorporated models must be compared to the outputs of other models. The models included in a forest planning system are constructed from several equations independently fitted to data. Often the models do not describe exactly the same tree population. The models are commonly formulated from the inventory data measured from different sample plots. In cases where the sample plots are the same, the measurements might have been made at different times.

By incorporating many models describing the same phenomena into a forest planning system the effects of differences noticed in the evaluation made at the tree level on the differences at the stand and forest area level can be analyzed. The comparison of the models can be made by ranking the outputs simulated for different forest structures. The ranking of the outputs must not depend on artifacts produced by the model (compare Stage 2003). If the ranking produced by the various models is the same, the results are probably correct in this respect. Thus, although the models may produce totally different absolute values, the relative differences between the outputs of the models might be rather similar.

Forest planning systems usually include an optimization part, which is used to select management schedules of stands according to specific goals and constraints. If the value of the goal or the constraint is estimated using different models describing the same phenomena, the effect of the differences in the outputs of the models on the optimization results can be analyzed. If the models produce biased estimates, a non-optimal alternative may be chosen or the true worth of the optimal solution may be overestimated. The solution may also be infeasible, if a constraint is used in the optimization. The overestimation of the effect of a specific treatment will cause the forest planning system to recommend that the treatment is carried out more frequently (Kangas and Kangas 1999).

1.5 Aims of the study

The aim of this study was to analyze, whether the available tree-level biomass (dry mass) models describing different components of living trees can be widely used in forestry modeling and analyses in Finland. This was the first attempt to systematize the evaluation of the set of biomass models describing the different components of a tree. The specific objectives were:

- To map representative models for the different tree components of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and silver (*Betula pendula)* and downy birch (*B. pubescens*) for Finnish conditions;
- To test the applicability of the most representative biomass models for trees having different sizes, growing on different sites and in different parts of Finland; and
- To analyze the use of these biomass models in the forestry modeling and analyses.

First, the availability of tree-level biomass models suitable for Finnish conditions was explored using literature. The representativeness of the models was studied by analyzing the modeling data, the division of a tree into different components, and the use of independent variables. Thereafter, the applicability of the most representative models for different sites and in different parts in Finland was tested by comparing the outputs of the models on fertile and infertile mineral soils, on mineral soils and peatlands, and in Southern and Northern Finland. In addition,

the use of the biomass models in MELA forest planning system was analyzed by implementing a case study. The case study helped to outline the effects of differences between the output of biomass models at the tree level on the differences between the outputs at the stand and forest area level in regard to biomass and net carbon sequestration of trees. Furthermore, if biomass was used as a constraint, the effects of differences between the outputs of biomass models on the optimization results, could be analyzed.

2 MATERIAL AND METHODS

2.1 Outlines of the study

In the first part of the study (chapters 3.1 and 3.2) the applicability of the selected tree-level biomass models for incorporation into forestry modeling and analyses were evaluated. The selection of the biomass models was made in three phases (Figure 1). In the first phase, the potential tree-level models for the incorporation into a forest planning system were selected from the available biomass models applicable for Finnish conditions. The models were chosen for different components of Scots pine, Norway spruce and birches. In the second phase, the most representative models were selected for the comparisons from these potential tree-level models. In the model comparisons the biomass was estimated by the selected sets of the models for the Finnish National Forest Inventory (NFI) sample trees. The outputs of the models were compared by tree species, by size of trees, by location (on mineral soils and on peatlands), and by site fertility (only on mineral soils). In addition, the outputs of the models for trees growing on mineral soils were compared to those for trees growing on peatlands. In the third phase, the applicability of the models for trees growing on mineral soils and on peatlands in different parts of Finland was determined (based on the comparisons carried out in the second phase).

In the second part of the study (chapter 3.3) the case study was implemented (Figure 2). In the case study the sets of models selected based on comparisons made in the first part of the study were incorporated into the MELA forest planning system (Siitonen et al. 1996, Redsven et al. 2004). Stand data from the forests of Finnish Forest Research Institute (FFRI) in Suonenjoki were used as input data in the MELA simulations. According to given simulation instructions the simulator part of the MELA produces different management schedules for each stand. From these the optimization part selects the optimal solution based on the set goals and constraints (Lappi 1992). In the case study, in each task the goal was to maximize the net present value (NPV) and, if a constraint was used, the constraint dealt with the biomass of trees.

Selection criteria (2.2):
- Models from the same data for biomass of stem wood, stem bark, living branches, foliage, dead branches, stump, roots
- Models for trees having large range in size
- Independent variables available from forest inventories or easily and relatively accurately estimated using models
- Models for trees growing on mineral soils and peatlands

Selection criteria (2.2):
- Representativeness of data (3.1.2)
- Division of a tree into components (3.1.3)
- Independent variables (3.1.4)

Comparisons:
- By tree species, by size of tree, by location (mineral soils and peatlands) (3.2.1-3.2.2)
- By site fertility (only mineral soils) (3.2.1)
- Between mineral soils and peatlands (3.2.2)

NFI data (2.3)

Exploration of tree-level biomass models (2.2)

Available tree-level biomass models for Finnish conditions (3.1.1)

Selection of the models (2.2)

Potential tree-level biomass models for incorporation into forestry modeling and analyses (3.1.1)

Selection of the models (2.2)

Models selected for the further evaluation (3.1.5)

Comparison of the outputs of the models (2.3)

Applicability of the biomass models for trees growing on different sites and different locations (3.2.3)

Figure 1. Outline of the first part of the study. The numbers of the chapters in which the different issues are discussed are shown in brackets.

The results of the MELA optimizations were analyzed by comparing the selected standwise management schedules inside each optimization task. If the sets of biomass models incorporated into the MELA produced different outputs, the use of the biomass of trees estimated by different sets of models as constraints in the optimization caused differences in the selection of optimal management schedules

inside each task. If the selection of optimal management schedules was the same irrespective of the set of biomass models used for the estimation of the constraint, the biomass estimates produced by the models were compared to each other inside the tasks. The comparisons between the different tasks were related to the net carbon sequestration of the trees. The incorporation of the biomass models into the MELA system, data for the MELA simulations and the analyses made using MELA are represented in more detail later in the context of the case study (see chapters 3.3.1 and 3.3.2).
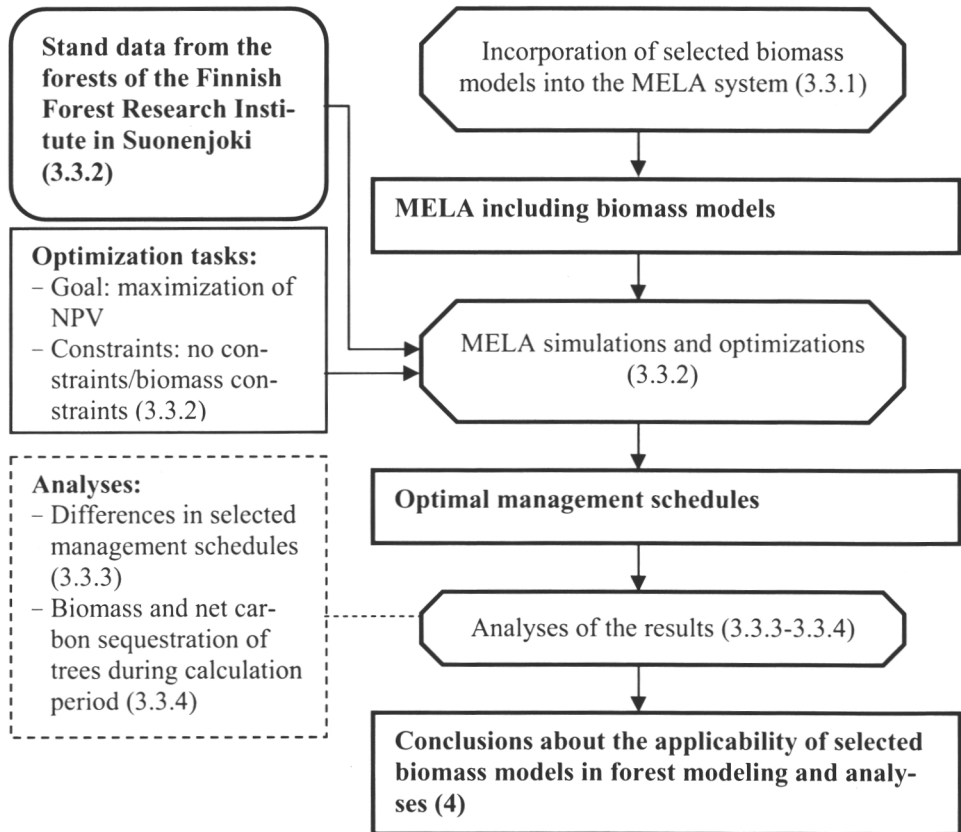
Figure 2. Outline of the second part of the study. The numbers of the chapters in which the different issues are discussed are shown in brackets.

2.2 Selection criteria for the comparison of tree-level biomass models

The literature was reviewed and available tree-level biomass models applicable to Finnish conditions were identified. From these models the potential tree-level models for forestry modeling and analyses were chosen for a closer assessment based on four selection criteria (Figure 1). First, the models should be based on the

same data for many, and preferably for all, components of a tree. The models should cover stem wood, stem bark, living branches, foliage, dead branches, stump and roots, because they were the smallest parts to be commonly modeled. If there were not, however, models for these components of a tree, the functions for the combinations of several components were taken into consideration. Second, the modeling data should comprise trees having large range in size. Third, the independent variables of the models should be available from the forest inventories, or they should be able to be easily and fairly accurately estimated using models. Fourth, the models for both mineral soils and peatlands should be included.

The selection of the models for further evaluation was based on more detailed study about the representativeness of the data used in the formulation of the models, the capability of the models to describe different components of a tree, and the capability of the used independent variables to describe the biomass of different components of a tree (Figure 1). The evaluation of the representativeness of the data covered the description of the study area (e.g. areal coverage, owner structure and resulting management intensity of forests included into the studies, number of stands, site fertility of the stands) and number and size of sample trees. The analysis of capability of the models to describe different components of a tree consisted of the study, to which components the models were formulated in different studies. The division and the definition of the different components of a tree were compared between the studies. The evaluation of the capability of the used independent variables to describe the biomass of different components of a tree was made by studying which independent variables were used, what kind of transformation for the variables were used and what were the effects of the use of these variables and transformations.

2.3 Data used for biomass estimations and comparisons of selected tree-level biomass models

The Finnish National Forest Inventory (NFI) data were used in order to estimate biomass of different components of a tree using selected models. The data origin from the 9th (NFI9) and the 8th inventory (NFI8) from Southern Finland, and from NFI8 from Northern Finland. The NFI8 data comprised the area of two Forestry Centers in the eastern part and NFI9 data the area of other parts of Southern Finland. Northern Finland was made up of the area of the three most northern Forestry Centers of Finland, and Southern Finland was made up of the other Forestry Centers. The used sample tree data were composed of measurements of 37 382 pines, 26 100 spruces and 14 275 birches with heights over 1.3 m and with a determined diameters at breast height. The sample tree characteristics are shown in more detail in Appendices 1, 2 and 3.

A preliminary study of the performance of the selected models was carried out. The sample tree data were divided into subgroups and classified into 1 cm diameter classes. The subgroups are shown in Figure 3. The biomass was estimated for the trees located on mineral soils and on peatlands. In the NFI data, the mineral soils were determined as soils having no peat in the organic layer and the amount of

peatland vegetation was less than 75%. On mineral soils the biomass was calculated for trees growing on fertile sites and infertile sites. The fertile sites were very rich sites, rich sites and damp sites; the other less fertile mineral soils were the infertile sites. The biomass was also estimated for trees growing on both mineral soils and peatlands in Southern Finland and in Northern Finland. By dividing the data into these subgroups it was possible to study the influence of forest structure on the reliability of the biomass estimates.
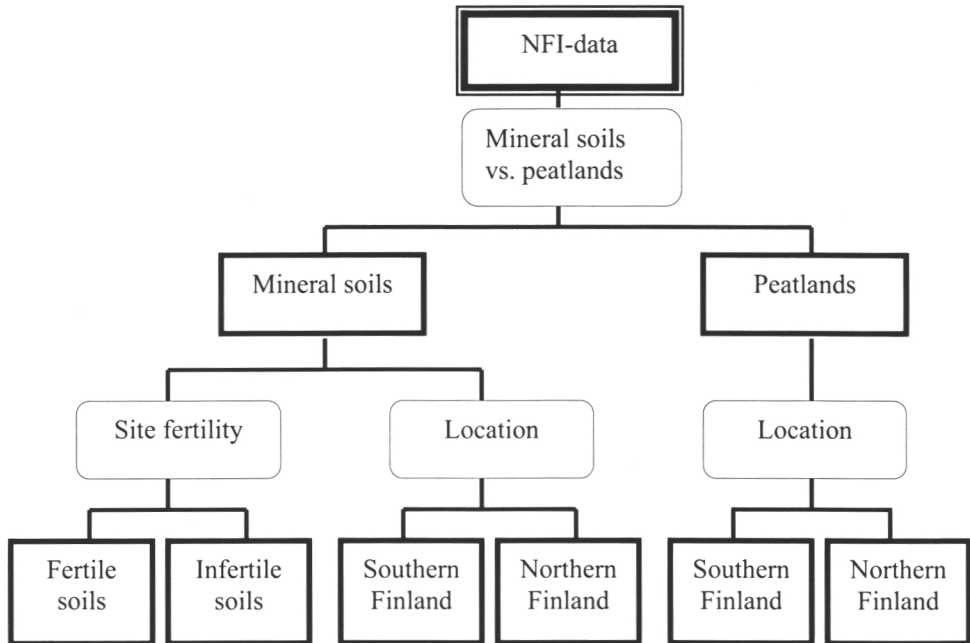
Figure 3. The criteria for the division of the data for different subgroups (boxes with thin lines) and the different subgroups, for which the biomass was estimated (boxes with bold lines).

After the division and the classification of the material, the mean values of biomass of different tree components were plotted against the diameter. Only every second diameter class was taken into account in the figures in order to clarify the differences. The differences of the outputs produced by selected models were compared with each other most closely on mineral soils and on peatlands. On mineral soils and on peatlands the standard deviations of biomass estimates within the diameter classes were determined in addition to mean values. In these subgroups the comparisons were made between the outputs of the models with respect to the ranking of biomass estimates of the studied tree species, and also with respect to the biomass estimates of trees representing single tree species in various diameter classes. If the mean biomass estimated using the selected models differed by more than 20% in diameter classes, the models were considered to produce different

results. On fertile and infertile mineral soils the results of selected biomass models were compared with each other, and also with the results of previous studies reported in the literature. An analysis was made of whether the biomass estimates of trees differed along the site fertility in the same diameter classes. The comparisons about the effects of location on the biomass estimates of trees were made on both mineral soils and on peatlands between Southern and Northern Finland. Furthermore, the outputs of the models for trees growing on peatlands were compared to those on mineral soils.

The allocation of the biomass to stem wood, stem bark, living branches, needles and dead branches was estimated using the selected sets of models that were found to be reasonable based on the preliminary study of the performance of the models. The biomass estimate of a component was studied in relation to the sum of the biomass estimates of above-ground components. The calculations were made only for trees growing on mineral soils. The trees were classified into 1 cm diameter classes and the range of proportions was studied separately for trees in three diameter classes: ≤ 20 cm; 21-40 cm; >40 cm.

3 RESULTS AND DISCUSSION

3.1 Pre-evaluation and selection of biomass models for more detailed evaluation

3.1.1 Potential tree-level biomass models for incorporation into forestry modeling and analyses

In Finland tree-level regression functions for the dry or green mass of different components of Scots pine and Norway spruce were derived by Hakkila (1967, 1969, 1971, 1972a, 1979), Issakainen (1988), Hakkila (1991), Finér (1989) and Laiho (1997). Also Mälkönen (1972), Hakkila et al. (1978), Korhonen and Maltamo (1990), Finér (1991) and Hakkila et al. (1995) have formulated some dry or green mass models for pine. The models for birch were formulated by Hakkila (1967), Mälkönen (1977), Simola (1977), Hakkila (1979), Björklund and Ferm (1982), Mälkönen and Saarsalmi (1982), Issakainen (1988), Finér (1989), Hakkila (1991), Saarsalmi et al. (1992) and Laiho (1997). Dependent on the study, the modeling data for birches comprised silver birch or downy birch or both of the birches together. In Finland the dry or green mass models for the components of some other deciduous trees have been made by Hakkila (1970), Simola (1977), Björklund and Ferm (1982), Björklund (1984), Saarsalmi and Mälkönen (1989) and Saarsalmi et al. (1991, 1992). In Sweden Albrektson (1980), Marklund (1987, 1988) and Petersson (1999) have made the most extensive studies about the biomass of a tree. Albrektson (1980) formulated tree-level regression functions for the dry mass of different components of Scots pine, Marklund (1987) for that of Norway spruce, and Marklund (1988) and Petersson (1999) for that of Scots pine, Norway spruce, and silver birch and downy birch together. Most of Marklund's

(1988) functions for spruce are the same as those published in a previous paper by Marklund (1987).

Marklund's (1988), Hakkila's (1991) and Korhonen and Maltamo's (1990) regression functions were chosen for the potential tree-level dry mass models for trees growing on mineral soils to be incorporated into the forestry modeling and analyses. However, excluded were those Marklund (1988) models having double bark thickness at breast height, relative bark thickness, crown radius, form quotient, diameter over bark of the thickest tree on a plot with radius 10 m, site index, north coordinate in the Swedish coordinate system, altitude or indicator variables about the thickness of humus layer, subsoil water level or surface/sub-surface water flow as independent variables. These variables are not commonly determined in the forest inventories, they cannot be estimated accurately, their range is different in Finland than in Sweden, or they are determined differently in the inventories in Finland than in Marklund's (1988) study. Hakkila's (1991) model for the biomass of living branches of pine – which has diameter at breast height, crown ratio and the height of living crown from the ground level as independent variables – produced unrealistic estimates according to preliminary calculations, and therefore it was excluded. In addition to Hakkila's (1991) models for the biomass of different components of a crown, Hakkila's (1979) functions for the wood density of stem over bark and that of stem wood and Hakkila's (1972a) models for the biomass of stump and roots were used in order to cover all components of a tree. The biomass of a stem could be estimated by multiplying the basic density with green volume of a stem. Hakkila's (1972a) models for the average stump and root biomass of a tree in the stands located in Southern and Northern Finland were selected for this study. Later in this text Marklund's (1988), Hakkila's (1972a, 1979, 1991) and Korhonen and Maltamo's (1990) models are referred to mineral soil models, although the modeling data might also include trees growing on peatlands. The mineral soil models selected for further evaluation are presented in Appendices 4, 5 and 6.

Compared to other available tree-level models the selected mineral soil models were derived from trees having wide range in size. In addition, the selected models were based on the same data for many components of a tree. Although also Albrektson's (1980) and Petersson's (1999) models fulfilled these demands, they were excluded from this study. Albrektson's (1980) models were derived only from pines growing in central Sweden. In addition, Albrektson (1980) had used variables (such as double bark thickness or current (3 years) volume growth), which were not commonly included in a forest planning system as independent variables. Some of Petersson's (1999) models contained north coordinate, east coordinate or altitude as independent variables. Therefore, these models cannot be used outside the area, for which the models were derived. In addition, one model had a variable describing the mineral soils and peatlands, and the classification of these sites differed from that used in Finland. Besides, Petersson (1999) used the same data for the formulation of the biomass models as Marklund (1988). Thus, the outputs of Petersson's (1999) and Marklund's (1988) models are not independent and the comparisons of the outputs of these models would not reveal reliable results about the variability of the biomass of a tree in the conditions outside the modeling data.

In Finland, Finér (1989, 1991) and Laiho (1997) have made the most extensive studies about the biomass of trees on peatlands. The dry mass models represented

in their studies were selected as potential models presenting trees growing on peat-lands. Finér (1989) has models both for unfertilized peatlands and fertilized peat-lands; the models for the unfertilized sites were chosen. Laiho (1997) has separate models for pines growing on undrained and drained peatlands, but only the models formulated for drained sites were selected. The models for fertilized and undrained peatland stands were excluded because most of the peatlands in Finland are unfer-tilized and drained (see Finnish Statistical Yearbook of Forestry 2003). Although Finér's (1989) models for dead branches of pine and a model for dead branches of spruce having only tree age as an independent variable would have fulfilled the selection criteria set for the biomass models, they were excluded from this study because tree age alone was not considered to reliably explain the variation of the biomass. Finér (1989) used the models for stump and roots earlier formulated by Issakainen (1988). These models were also used in this study. The peatland models chosen for further evaluation are presented in Appendices 7 and 8.

3.1.2 Representativeness of the data used for the formulation of biomass models

The data for the selected mineral soil models were collected at the end of the 1960s and the beginning of the 1970s, and in the 1980s. Excluding Korhonen and Mal-tamo's (1990) models the sampling comprised stands from wide range of latitudes. The data were collected mainly from the forests owned by state, Finnish Forest Research Institute, forest companies and communities. Some studies were based on NFI data. The sampling comprised many stands (or sample plots) from different site fertilities. The data consisted of many sample trees with wide size ranges.

The data for the selected peatland models were collected in the 1980s and at the beginning of the 1990s. The sample consisted of single peatland stands from a very small area. The number of sample trees was small and the size range of sample trees did not cover the whole size range of trees growing on peatlands. The descrip-tion of the modeling data of the mineral soil models is presented in detail in Table 1, and that of the peatland models in Table 2.

Marklund's (1988) biomass functions are commonly used for the biomass cal-culations in Scandinavia (e.g. Hoen and Solberg 1994, Mäkipää et al. 1999, Mink-kinen et al. 2001), but their applicability for different conditions has not been dis-cussed much. The detailed evaluation of the representativeness of the data used for the formulation of the biomass models revealed some defects, which have to be taken into account when the models are applied. The functions were valid in the range 0-45 cm in pine, 0-50 cm in spruce and 0-35 cm in birch, and they behaved logically up to 100 cm in breast height diameter (Marklund 1988). Although the data of Marklund's (1988) models covered a wide diameter range of trees growing in Sweden, there are certain factors that might affect the results when applying the models in Finland. In Marklund's (1988) material the fertility of sites and the struc-ture of stands were not the same as in Finland. In the southern part of Sweden

Table 1. Description of the data used for formulation of the mineral soil models.

	Marklund (1988)	Hakkila (1972a)	Hakkila (1979)	Hakkila (1991)	Korhonen and Maltamo (1990)
Study period	1983-1985	1969-1971	Mainly 1968-1970	1984-1986	1988-1989
Study area	Whole Sweden	Southern and Northern Finland	Whole Finland	Whole Finland	The most southern Finland
Sampling	Selected from forests belonging to Swedish Forest Service.	Forest owned by forest companies and Finnish Forest Research Institute	Part of the 5th National Forest Inventory, supplemented data from the Forest Service and Finnish Forest Research Institute	Mainly from stands owned by forest companies, stands marked for cutting	Forests owned by states and communities, selected from one time measured sample plots of the 8th National Forest Inventory
Number of stands	131	10	Not documented	130	Not documented
Site fertility	Different site fertilities	Different site fertilities (most fertile sites were not included)	Different site fertilities	Different site fertilities	Different site fertilities
Tree species	Scots pine Norway spruce Silver and downy birch	Scots pine Norway spruce	Scots pine Norway spruce Silver and downy birch	Scots pine Norway spruce Silver and downy birch	Scots pine
Type of sample trees	Felled trees	Felled trees	Standing and felled trees	Felled trees	Felled trees

Number of sample trees	**Determination of dry mass:** Pine: 493 Spruce: 551 Birches: 242 **Stump and roots:** Pine: 315 Spruce: 341	Pine: 224 Spruce: 273	**Standing trees:** Pine: 1643 Spruce: 1368 Birches: 310 **Felled trees:** Pine: 150 Spruce: 166 Birches: 40	**Sample trees for green mass:** Pine: 2685 Spruce: 2234 Birches: 1468 **Trees for determining moisture and needle mass:** Pine: 283 Spruce: 218	Pine: 121
Size of sample trees	**Height:** Over 1.3 m	**Mean stump height diameter:** Pine: 28 cm Spruce: 26 cm (15-70 cm)	**Mean breast height diameter of standing trees:** Pine: 21 cm Spruce: 19 cm Birches: 16 cm	**Range of breast height diameters:** Pine: 5 - 40 cm Spruce: 5 - 43 cm Birches: 4 - 41 cm	**Range of breast height diameters:** Pine: 5 - 45 cm
Modeled components used in the current study	Stem wood Stem bark Living branches Needles Dead branches **Pine and spruce:** Stump Roots	Stump and roots	Stem over bark Stem wood	Living branches Needles Dead branches	Stem wood Stem bark Living branches

Table 2. Description of the data used for formulation of the peatland models.

	Issakainen (1988)	Finér (1989)	Finér (1991)	Laiho (1997)
Study period	Measurements in 1986	Measurements in 1985	1984 and 1987	1991-1992
Study area	Eastern Finland	Eastern Finland	Eastern Finland	South-west Finland
Sampling	Experiments in same drainage area each at different site	Experiments in same drainage area each at different site	One drainage area	Sites having varying drainage ages
Number of stands	3	3	1	4
Site fertility	An ordinary sedge pine mire (VNRmu) A herb-rich sedge pine mire (RhNRmu) A *Vaccinium myrtillus* spruce mire (MKmu)	An ordinary sedge pine mire (VNRmu) A herb-rich sedge pine mire (RhNRmu) A *Vaccinium myrtillus* spruce mire (MKmu)	An ombrotrophic bog (IR)	Tall-sedge pine fens
Tree species	Scots pine (VNRmu, RhNRmu) Norway spruce (MKmu) Silver and downy birch (RhNRmu)	Scots pine (VNRmu, RhNRmu) Norway spruce (MKmu) Silver and downy birch (RhNRmu)	Scots pine	Scots pine Norway spruce Downy birch
Type of sample trees	Felled trees	Felled trees	Felled trees	Felled trees
Number of sample trees	Pine: 16 Spruce: 8 Birches: 8	Pine: 8 in both sites Spruce: 9 Birches: 7	Pine: 27	Pine: 33 Spruce: 8 Birch: 17
Size of sample trees	**Range of breast height diameters:** Pine: 5-25 cm Spruce: 7-30 cm Birches: 6-23 cm	**Range of breast height diameters:** Pine: 6-22 cm (VNRmu), 9-24 cm (RhNRmu) Spruce: 6-37 cm Birches: 8-21 cm	**Range of breast height diameters:** Pine: 5-22 cm	**Mean breast height diameters:** Pine: 15 cm Spruce: 6 cm Birch: 7 cm
Modeled components used in the current study	Stump and roots	Stem wood Stem bark Living branches Needles, leaves Dead branches	Stem wood Stem bark Living branches Needles Dead branches Stump and roots	**Pine and birch:** Stem wood Stem bark Living branches Needles, leaves Dead branches **Spruce:** Stem over bark

the sites are more fertile and the growing period is much longer, and in the northern part of Sweden trees grow at higher altitudes than in Finland. In addition to this, the sample trees were selected from forests owned by the Swedish Forest Service, whose way to manage forests may be different than that of forest owners in Finland. According to Marklund (1988) the conditions, which were poorly repre-

sented in the material, were coastal areas, forests at high altitudes, forests under extreme management regimes, and seriously damaged trees (Table 3).

Another set of models, which has often been used for the estimation of the biomass of trees in Finland (e.g. Mielikäinen et al. 1995, Hynynen 2001, Malinen et al. 2001), is Hakkila's (1979 and 1991) models. In Hakkila's (1979) study models for the wood density of stems were formulated separately for the trees having heights 2.5-7.4 m and for the trees having heights more than 7.4 m. In this study, the data for determining the wood density of stem at breast height were collected as part of the 5th Finnish National Forest Inventory (NFI5). The same data were used as a part of the data, from which Laasasenaho's (1982) volume functions were derived. The largest defects of Hakkila's (1979) data are that the number of birches growing in Northern Finland is small, and the average size of pines used for wood density determination in Northern Finland is large. The NFI5 data were supplemented with material collected from the forest of the Forest Service and the Finnish Forest Research Institute. This supplementary data collected from felled sample trees were used for the construction of equations that predict the average stem wood density of standing trees from the wood density of increment core bored at breast height (1.3 m). The characteristics of these sample trees are not well documented, but according to Hakkila (1979) the data corresponded relatively well to the NFI5 data in its average measurements. The change of the structure of forests since the NFI5 may have effects on the current form of the stems and the crowns.

Hakkila (1991) has presented models for different components of crown. In Hakkila's (1991) study the sample tree data consisted of trees having a diameter at breast height of at least 4 cm and at most 43 cm. Therefore, the whole diameter range of trees growing in Finland is not covered. The data represent the trees felled in thinnings and in final fellings. The trees cut in thinnings are often more suppressed than the trees left in the stand, and therefore, the data were biased. Hakkila's (1991) material was collected mainly from the forests owned by companies and thus, the structure of the material was biased also in this respect. The sampling was deficient in the coastal areas in Western Finland and in the forests in the most northern part of the country. In Northern Finland especially, there was a poor representation of spruce stands in the first thinning phase, and birch stands in the first thinning and subsequent thinning phases (Table 3).

In Hakkila's (1972a) study the dry mass of 50 stumps was determined only in seven sample stands in Southern Finland and in three sample stands in Northern Finland (Table 3). The stands were in clear-cutting areas and the material comprised the stumps of pines and spruces, whose range of stump diameter was 15-70 cm. However, according to Hakkila (1972a) only 15-50 cm could be accepted as the range of application of the results. In order to determine the correlation between stump height diameter and breast height diameter, 50-100 trees were measured from corresponding stands in the immediate vicinity of each sample stand. The regression functions were derived for the stump height diameter from the breast height diameter.

In Finland Korhonen and Maltamo (1990) formulated models for stem wood, stem bark and living branches of pines. The sample plots were selected NFI8 sample plots located in the forests owned by state or communities in the most southern

Table 3. Summary of advantages and disadvantages of the modeling data.

Advantages	Disadvantages
Marklund (1988)	
− Data covers wide diameter range	− Data from Sweden
− Regional representativeness rather good	− Data only from forest owned by Swedish Forest Service
− Data covers trees growing on different site fertilities	− Coastal areas, forests at high altitudes, forest under extreme management regimes and seriously damaged trees poorly represented
Hakkila (1972a, 1979, 1991)	
Stem wood and crown:	*Stem wood:*
− Regional representativeness rather good	− Size range of sample trees not documented
− Data covers trees growing on different site fertilities	− Number of birches growing in Northern Finland small
	− Average size of pines large in Northern Finland
Crown:	*Crown:*
− Data covers rather wide diameter range	− Data do not cover the thinnest and the thickest trees
	− Data represent only trees felled in cuttings
	− Data only from forests owned by forest companies
	− Sampling defective in the coastal areas in Western Finland and in the forests in the most northern part of Finland
Stump and roots:	*Stump and roots:*
− Data from Southern and Northern Finland	− Data only from single regions
	− Data from single clear cutting areas
	− Data emphasized to upper diameter classes
	− Most fertile sites not included
	− Data only from forests owned by forest companies and Finnish Forest Research Institute
Korhonen and Maltamo (1990)	
− Data covers rather wide diameter range	− Smallest trees not represented in the data
− Data covers trees growing on different site fertilities	− Material only for pine
	− Data covers only the most southern part of Finland
	− Infertile sites are over-represented
	− Data only from forests owned by state and communities
Finér (1989, 1991), Issakainen (1988)	
− Data collected from peatlands	− Data only from Eastern Finland
	− Data from single peatlands
	− Number of sample trees small
	− Data covers only a narrow range of diameter
Laiho (1997)	
− Data collected from peatlands	− Data only from South-west Finland
	− Data from single peatlands
	− Number of sample trees small
	− Mean diameter of sample trees small

part of Finland. The material of the models comprised only sample trees of pines. The infertile sites were stressed in this material, and the smallest trees were not included in the study (Table 3).

The modeling data for Finér's (1989, 1991) and Issakainen's (1988) studies were collected from single peatlands stands located in Eastern Finland. In Laiho's (1997) study the study areas were located in South-west Finland. In all these stud-

ies, the number of sample trees was small and the sample trees covered only a very narrow range of diameters (Table 3).

3.1.3 Capability of the models to describe different components of a tree

Only a few of studies considered the biomass of all components of a tree (Tables 1 and 2). Neither Marklund's (1988) nor Hakkila's (1972a, 1979, 1991) studies included biomass models for birch leaves. Korhonen and Maltamo (1990) had derived models only for stem wood, stem bark and living crown of pine. Generally, for the biomass of the stump and the roots of birch there were no representative tree-level models that could be used for the large-scale calculations. Also the models for fine roots and inflorescences were lacking. Moreover, only Finér (1989, 1991) had separate models for cones, but the models were excluded from this study, because they were derived from a very small amount of sample trees and it was not possible to compare them with other considered studies.

Even if the models were available for all the components of a tree, the comparison of the models would not be easy, because the division or the definition of the components vary in different studies. Especially, the comparison of the biomass of the stump estimated by different models is problematic, because the height of the stump and the separation of the stump from the roots vary from one study to another. When the determination of the stump varies, it also affects the biomass of stem wood, stem bark and roots. In Marklund's (1988) study the cutting heights of sample trees were determined as 1% of the tree height measured from the ground level. In Hakkila's (1972a), Hakkila's (1979), Korhonen and Maltamo's (1990) and Finér's (1989, 1991) works it could be supposed that the trees were cut as close to the ground as possible. Issakainen (1988) and Laiho (1997) had not described the point of cutting properly. Each model for roots describes a different proportion of the whole biomass of the roots because the diameters of roots taken to the formulation of the model differs from one study to another. Marklund (1988) had formulated separate functions for roots having a diameter of <5 cm, and roots having a diameter of ≥5 cm. The roots, which had diameter <5 cm, consisted only of those roots that remained attached when the stump-root system was lifted from the ground. The functions for roots ≥5 cm consisted only of the trees that had such big roots. In Hakkila's (1972a) study, an attempt was made to extract all the roots having a minimum diameter of 5 cm; however, some thicker roots were left in the ground. Hakkila (1972a) presented joint functions for the biomass of stump and roots. Moreover, Issakainen's (1988) and Finér's (1991) functions were based on roots with diameters of >1 cm.

The division of stem was not consistent in the considered studies. Marklund (1988), Finér (1989, 1991) and Korhonen and Maltamo (1990) presented biomass models for both stem wood and stem bark. Laiho (1997) presented models for both stem wood and stem bark of pine and birch, but only a model for stem over bark of spruce. Hakkila (1979) formulated models for the basic density of stem wood and stem over bark, but had no models for stem bark (Table 4).

Table 4. Summary of advantages and disadvantages of the models concerning the division of a tree into different components.

Advantages	Disadvantages
Marklund (1988)	
– *Pine and spruce*: models for all components of a tree (excluding the thinnest roots)	– *Pine and spruce*: no separate models for living branches excluding needles, no separate models for cones, no models for the thinnest roots
– *Pine, spruce and* birch: separate models for stem wood and stem bark	– *Birch*: no models for leaves, stump and roots
	– *Pine, spruce and birch*: no separate models for inflorescences
Hakkila (1972a, 1979, 1991)	
– *Pine and spruce*: models for all components of a tree (excluding the thinnest roots)	– *Pine, spruce and birch*: no models for all components of a tree derived from the same material, no separate models for stem bark, no separate models for inflorescences
	– *Pine and spruce*: no separate models for stump and roots, no models for the thinnest roots, no separate models for living branches excluding needles, no models for cones
	– *Birch*: no models for leaves, stump and roots
Korhonen and Maltamo (1990)	
– *Pine:* separate models for stem wood and stem bark	– *Pine*: no separate models for needles, for cones and for inflorescences, no models for dead branches, for stump and for roots
	– *Spruce and birch*: no models
Finér (1989, 1991), Issakainen (1988)	
– *Pine, spruce and birch*: models for all components (excluding the thinnest roots), separate models for stem wood and stem bark, separate models for foliage and living branches excluding foliage	– *Pine, spruce and birch*: no separate models for stump and roots, no models for the thinnest roots and for inflorescences
– *Pine and spruce*: separate models for cones	
Laiho (1997)	
– *Pine and birch*: models for all above-ground components, separate models for stem wood and stem bark, separate models for foliage and living branches excluding foliage	– *Spruce*: model only for stem over bark
	– *Pine and birch*: no models for stump and roots, no models for inflorescences
	– *Pine*: no models for cones

The division of the biomass of living branches also differed between studies. Korhonen's and Maltamo's (1990) models were derived only for living branches including needles. In Marklund's (1988) and Hakkila's (1991) models, biomass of living branches including needles and biomass of needles have been modeled separately. There is no separate model for living branches excluding needles. As a comparison, Finér (1989, 1991) and Laiho (1997) have separate biomass models for foliage and living branches excluding foliage (Table 4). Marklund (1987) describes the sampling used in Marklund (1988). Marklund (1987) had defined living branches as lignified branches longer than 10 cm including attached dead parts. In other studies the term living branches was not clearly defined, and thus, the segregation of living branches from dead branches was not clear.

The modeling of biomass of dead branches was also problematic. Marklund's (1988) functions for dead branches had been derived from the trees that had dead branches. In other studies it was not documented whether all sample tree had dead branches. The definition of dead branches was unclear in all considered studies.

3.1.4 Capability of used independent variables to describe the biomass of different components of a tree

In all selected biomass models the diameter at breast height was used as an independent variable. The breast height diameter explained most of the variation in the biomass of different components of a tree (Appendices 4-8). Tree height was also commonly used as an independent variable in the models (Table 7). The reliability of the biomass functions increased when the tree height was taken as an independent variable in addition to breast height diameter. In addition, crown length, crown ratio or height of living crown limit was used in some models to describe the biomass of living branches, dead branches or foliage. In single models, biological age, age at breast height and variables describing the growing conditions (climatic zone, site fertility, relative height of a tree) were used. The relations between the independent variables have been used in order to describe, for example, diameter growth, height growth and stem form. All these variables increased the value of the multiple correlation coefficient, but their significance was much lower than that of breast height diameter. The use of independent variables for different components of a tree in the mineral soil models is presented in Table 5, and that in the peatland models in Table 6.

Marklund's (1988) models can be presented in the general formula

$$\ln(m) = \alpha * (d/(d + \beta)) + \gamma * h + \delta * \ln(h) + \zeta * \ln(l_c) + \varepsilon \tag{1}$$

where

	m	= Dry mass of a component (kg)
	$\alpha, \beta, \gamma, \delta, \zeta$	= Parameters
	ε	= Error term
	d	= Diameter at breast height (1.3 m) (cm)
	h	= Height (m)
	l_c	= Length of living crown (m)

All Marklund's (1988) functions have a logarithmically transformed dependent variable (base e) (Appendix 4). Because of this transformation, the functions only produce positive values. The expression $d/(d+\beta)$ (where d = breast height diameter, β = constant) is used in all Marklund's functions. This expression restricts the rise of the curves and yields reasonable estimates also for the thickest trees (Marklund 1987). There were models that included tree height as an independent variable (in addition to diameter at breast height) for all the above-ground components except for the living branches of birch (Table 7). The tree height is used as an independent variable either without any transformation or with logarithmic transformation. Crown length has been used as an independent variable in some functions of biomass of needles and dead branches of spruce. In these functions the crown length has been transformed logarithmically.

Table 5. Components and independent variables of mineral soil models.

Tree species	Components of tree	Independent variables
Marklund (1988)		
Scots pine, Norway spruce	Stem wood, stem bark, living branches (including needles), needles, dead branches, stump, roots	Diameter at breast height
	Stem wood, stem bark, living branches (including needles), needles, dead branches	Diameter at breast height, height of a tree
Norway spruce	Needles, dead branches	Diameter at breast height, height of a tree, crown length
Silver and downy birch	Stem wood, stem bark, living branches (excluding leaves), dead branches	Diameter at breast height
	Stem wood, stem bark, dead branches	Diameter at breast height, height of a tree
Hakkila (1972a, 1979, 1991)		
Scots pine, Norway spruce	Living branches (including needles), needles, dead branches	Diameter at breast height
	Living branches (including needles)	Diameter at breast height, height of a tree
	Needles	Diameter at breast height, crown ratio
	Stem over bark, stem wood (separate models for the basic density of small and tall trees)	Diameter at breast height, height of a tree, age at breast height, (volume of a stem over bark or without bark), climatic zone
	Stump and roots	Stump diameter over bark base (converted to diameter at breast height)
Norway spruce	Living branches (including needles)	Diameter at breast height, height of a tree, crown ratio
Silver and downy birches	Living branches (excluding foliage), dead branches	Diameter at breast height
	Living branches (excluding foliage)	Diameter at breast height, height of a tree, crown ratio
	Stem over bark, stem wood (separate models for the density of small and tall trees)	Diameter at breast height, age, (volume of a stem over bark or without bark)
Korhonen and Maltamo (1990)		
Scots pine	Stem wood, stem bark	Diameter at breast height, height of a tree
	Living branches (including needles)	Diameter at breast height, height of tree, length of living crown
	Stem wood	Diameter at breast height, height of a tree, biological age
	Stem bark	Diameter at breast height, height of a tree, site fertility

According to Marklund's (1988) functions the biomass of tree components increases with diameter at breast height for all tree species. The biomass of stem wood and that of stem bark for all tree species increases with the tree height, when the diameter at breast height is constant. According to the functions, the biomass of living branches is larger in short than in tall pines and spruces, when the trees having same diameters are considered. A function for the biomass of needles of

Table 6. Components and independent variables of peatland models. RhNRmu = herb-rich sedge pine mire, VNRmu = ordinary sedge pine mire, IR = ombrotrophic bog, MKmu = *Vaccinium myrtillus* spruce mire.

Tree species	Components of tree	Independent variables
Finér (1989) (RhNRmu)		
Scots pine	Stem wood, stem bark, living branches (excluding needles), needles, dead branches	Diameter at breast height
Silver and downy birch	Stem wood, stem bark, living branches (excluding foliage), leaves	Diameter at breast height
	Dead branches	Diameter at breast height, crown ratio
Finér (1989) (VNRmu)		
Scots pine	Stem bark, living branches (excluding needles), needles, dead branches	Diameter at breast height
	Stem wood	Diameter at breast height, height of a tree
Finér (1991) (IR)		
Scots pine	Stump and roots, dead branches	Diameter at breast height
	Stem wood, stem bark	Diameter at breast height, height of a tree
	Living branches (excluding needles), needles	Diameter at breast height, crown ratio
Finér (1989) (MKmu)		
Norway spruce	Stem bark, dead branches	Diameter at breast height
	Stem wood	Diameter at breast height, height of a tree
	Living branches (excluding needles), needles	Diameter at breast height, crown ratio
Issakainen (1988)		
Scots pine, Norway spruce, silver and downy birch	Stump and roots	Diameter at breast height
Laiho (1997)		
Scots pine	Stem wood, stem bark	Diameter at breast height, height of a tree
	Living branches (excluding needles), needles	Diameter at breast height, height of crown limit
	Dead branches	Diameter at breast height, relative height of a tree
Norway spruce	Stem over bark	Diameter at breast height, height of a tree
Silver and downy birches	Leaves	Diameter at breast height
	Stem wood, stem bark, dead branches	Diameter at breast height, height of a tree
	Living branches (excluding foliage)	Diameter at breast height, relative height of a tree

pine has both height and logarithmic height as independent variables. The effect of the logarithmic height is larger on the value of the function, and thus, for trees in the same diameter class the shortest pines have the largest biomass of needles. The biomass of needles is also larger in short than in tall spruces, when the trees having

the same diameters at breast height and the same lengths of crowns are studied. The increase in the logarithmic transformed crown length results in an increase in the biomass of needles of spruce when the height and diameter are considered as constants. In the function for dead branches of pine and birch, the influence of height and logarithmic height is contradictory. The height has only a small effect on the biomass of dead branches of pine in a certain diameter class. When the breast height diameter is constant and the tree height is less than 10 m, the tall birches have larger biomass of dead branches than short birhces. For birches equal to or taller than 10 m, the function for dead branches produces larger biomass in short than in tall trees in the same diameter class. A function for the biomass of dead branches of spruce has height, logarithmically transformed height and logarithmically transformed crown length as independent variables. The function produces the largest biomass of dead branches for the tallest spruces, when the spruces have the same breast height diameters and the same crown lenghts. When spruces have the same diameters and heights, the biomass of dead branches is larger in trees having shorter crowns.

The general formulas of Hakkila's (1972a, 1979, 1991) models are for stem,

$$m = (\alpha * (d/t)^2 + \beta * \ln(h/d) + \gamma * \ln(h/t) + \delta * h \ldots + \varepsilon) * k * z * V_o \tag{2}$$

for different components of crown

$$\ln(m) = \alpha * \ln(d) + \beta * \ln(h) + \gamma * cr + \delta * (d/h^2) + \zeta /h^2 + \varepsilon \tag{3}$$
$$m = \alpha * d + \beta * d^2 + \gamma * d^3 + \delta * (d^3/h) + \zeta * d^3 * cr + \eta * d * cr^2 + \varepsilon \tag{4}$$

and for stump and roots (Hakkila's (1972a) function is converted into the formula, in which breast height diameter is used instead of stump diameter (see Hakkila 1972a))

$$m = \alpha * (d/\beta)^2 + \varepsilon \tag{5}$$

where		
	m	= Dry mass of a component (kg)
	$\alpha, \beta, \gamma, \delta, \zeta, \eta$	= Parameters
	ε	= Error term
	cr	= Crown ratio
	d	= Diameter at breast height (1.3 m) (cm or mm)
	h	= Height (m or dm)
	k	= Correction term for knots and bark
	t	= Age at breast height (years)
	V_o	= Stem volume with or without bark (m^3)
	z	= Correction term for climatic zone

In most of the models presented in Hakkila (1991) and in all of the models presented in Hakkila (1972a, 1979), the dependent variables have not been transformed (Appendix 5). The logarithmic transformation (base e) has been used in some functions for the biomass of living branches and needles. In Hakkila's (1979, 1991) models the independent variables and the transformation varies considerably

among tree species (Table 7). When the basic density of stem wood is considered, they also vary between short and tall trees. Hakkila (1979) formulated multiple regression equations for the density of stem wood separately for trees having heights of 2.5-7.4 m, and for trees having heights >7.4 m. The independent variables used in the equations are age at breast height, diameter at breast height, tree height, diameter growth, height growth, volume, and the relations between height and diameter, age and height, and age and diameter.

In the results reported below about the variation of basic density of stem according to Hakkila's (1979) functions, it is assumed that the independent variables other than the considered ones are constants. According to Hakkila's (1979) functions, the basic density of stem of pine is small in trees having large height growth rate, when other variables represented in the functions are constant. The tall and thin pines have high basic density of stem. In the functions for short pines (2.5-7.4 m) large diameter growth means low basic density of stem wood. According to the functions for short pines, the tallest trees have the greatest basic density of stem. In the functions for tall pines (>7.4 m), large value of the relation between age at breast height and tree height means large basic density. The basic density of stem wood of spruce is larger in tall than in short trees, when the age at breast height, diameter growth and volume of stem are constant. When other variables are constant, the basic density of stem wood of spruce is the smallest in the oldest trees. Furthermore, the basic density is the largest in spruces having the smallest diameter growth. According to Hakkila's (1979) functions, the old birches have a larger basic density of stem wood than the young birches in the same diameter class.

Hakkila (1991) has presented models having only breast height diameter as an independent variable for the biomass of living branches, and that of dead branches of all considered tree species and for the biomass of needles of pine and spruce. Hakkila (1972a) also has models having breast height diameter as an independent variable for the biomass of stump and roots of pine and spruce. In all these models the breast height diameter is positively correlated with the biomass. In some of Hakkila's (1991) functions for living branches of birch and spruce, height and crown ratio has also been used. According to the functions, the biomass of living branches of birch and spruce is smaller in tall than in short trees when the trees have the same diameters at breast heights and the same crown ratios. When the height and diameter are constant, the biomass of living branches is the largest in trees having the largest crown ratio. According to a Hakkila's (1991) function, for trees in the same diameter class, the biomass of living branches of pine depends on the tree height and the relation between breast height diameter and height. According to some of Hakkila's (1991) functions for needles of pine and spruce, in the same diameter class the biomass of needles is the largest in trees having the largest crown ratio.

The formulation of some Hakkila's (1972a, 1991) functions set limitations for the use of the models for the smallest trees. The functions having dependent variables, which are not transformed logarithmically and having only breast height diameter as an independent variable produce negative values for the biomass of the thinnest trees.

The general formula of Korhonen and Maltamo's (1990) biomass models for pine is

$$\ln(m) = \alpha * \ln(d^2) + \beta * \ln(d) + \gamma * \ln(h) + \delta * \ln(t_b) + \zeta * d^2 + \eta * l_c + \theta * CT + \varepsilon \ (6)$$

where m = Dry mass of a component (kg)

                $\alpha, \beta, \gamma, \delta, \zeta, \eta, \theta$ = Parameters

                ε = Error term

                CT   = Dummy variable. CT = 1, if a tree grows on CT sites, otherwise CT = 0

                d = Diameter at breast height (1.3 m) (cm)

                h = Height (m)

                l_c = Length of living crown (m)

                t_b = Biological age (years)

All dependent variables and most of the independent variables of Korhonen and Maltamo's (1990) models are logarithmically transformed (Appendix 6). Korhonen and Maltamo (1990) used diameter at breast height and height as independent variables in all functions. In addition, biological age is used in a function for biomass of stem wood, and crown length in the biomass function for living branches. A dummy variable describing the site fertility is included into a function for the biomass of stem bark.

According to Korhonen and Maltamo's (1990) models, the biomass of stem wood and that of stem bark are larger in tall than in short trees in the same diameter classes. When the diameter at breast height and tree height are constant, the biomass of stem wood is also larger in old than in young trees in the same diameter class. According to Korhonen and Maltamo's (1990) function, the biomass of living branches is smaller in tall than in short trees, when the trees have the same diameters and the same crown lengths. The long living crown produces higher biomass of living branches than the short living crown, when the trees having same sizes are considered.

Finér's (1989, 1991) and Issakainen's (1988) models follow the formula

$$\ln(m) = \alpha * \ln(d) + \beta * d + \gamma * \ln(h) + \delta * \ln(cr) + \varepsilon \qquad (7)$$

where m = Dry mass of a component (kg or g)

                $\alpha, \beta, \gamma, \delta$ = Parameters

                ε = Error term

                cr   = Crown ratio

                d = Diameter at breast height (1.3 m) (cm)

                h = Height (m or dm)

In Finér's (1989, 1991) equations a logarithmic transformation was used for the calculations of all dependent variables and almost all the independent variables (Appendix 7). Finér (1989, 1991) used breast height diameter or logarithmic breast height diameter with or without logarithmic height as an independent variable in the regression equations. Logarithmically transformed crown ratio was also included in some of the functions describing the biomass of different components of crown.

Table 7. Summary of advantages and disadvantages of the models concerning the use of independent variables and the estimation of dependent variables.

Advantages	Disadvantages
Marklund (1988)	
Independent variables	**Independent variables**
– *Diameter*: stem wood and stem bark, all components of crown of all studied tree species, stump and roots of pine and spruce	– *Diameter*: no models for stump and roots of birch
– *Diameter and height:* stem wood and stem bark, all components of crown of pine and spruce, stem wood, stem bark and dead branches of birch	– *Diameter and height*: no model for living branches of birch
– Expression $(D/(D+\beta))$ restricts the rise of the curve and yields reasonable estimates also for the thickest trees	– *Diameter, height and crown ratio*: models only for needles and dead branches of spruce
Dependent variables	
– Can only get positive values	
Hakkila (1972a, 1979, 1991)	
Independent variables	**Independent variables**
– *Diameter*: all modeled components of a crown of all studied tree species, stump and roots of pine and spruce	– The use of independent variables of basic density of stem varies between tree species and between different sizes of trees
	– *Diameter, height and crown ratio*: use of these variables varies between different crown components
Dependent variables	**Dependent variables**
– *The models for living branches and needles have logarithmically transformed dependent variables (see Appendix 5)*: they can only have positive values	– *Dependent variable not logarithmically transformed and only breast height diameter as an independent variable*: negative values for the thinnest trees
Korhonen and Maltamo (1990)	
Independent variables	**Independent variables**
– *Diameter and height*: stem wood and stem bark of pine	– Not same independent variables for all modeled components
Dependent variables	
– Can only have positive values	
Finér (1989, 1991), Issakainen (1988)	
Independent variables	**Independent variables**
– *Diameter*: stem wood and stem bark, stump and roots of all studied tree species, all components of a crown of pine, dead branches of spruce, living branches and leaves of birch	– *Diameter*: not models for all components of a crown of spruce and birch
– *Diameter and height*: stem wood and stem bark of pine, stem wood of spruce	– *Diameter, height, crown ratio*: use varies between different components
Dependent variables	
– Can only have positive values	
Laiho (1997)	
Independent variables	**Independent variables**
– *Diameter and height*: stem wood and stem bark of pine and birch, stem over bark of spruce, dead branches of birch	– Not possible to get models having same independent variables for all components of a tree
Dependent variables	
– Can only have positive values	

In Finér's (1989, 1991) functions the biomass of all components increases with breast height diameter, when other variables used in the functions are constant. According to functions for the stem wood of pine and spruce, in the same diameter class the biomass is larger in tall than in short trees. In a function for biomass of stem bark of pine, logarithmic tree height has been used as an independent variable. The effect of logarithmic height is that the biomass of stem bark is the smallest in the tallest pines in the same diameter class. According to functions for the biomass of living branches and those for needles, in the same diameter class the biomass is the largest in pines and spruces having the largest crown ratio. The biomass of dead branches of birch trees in the same diameter class increases as the crown ratio decreases.

The general formula of Laiho's (1997) models is

$$m = \alpha * d^\beta * h^\gamma * l_{cl}^\delta * h_{rel}^\zeta \tag{8}$$

where   m   = Dry mass of a component (kg)
         $\alpha, \beta, \gamma, \delta, \zeta$ = Parameters
         d   = Diameter at breast height (1.3 m) (cm)
         h   = Height (m)
         h_{rel} = Relative height of a tree, the height of a tree in rela-
                                tion to the dominant height of a trees
         l_{cl} = Crown limit (m)

Laiho (1997) has not used any transformations for the dependent variables (Appendix 8). Laiho's (1997) regression functions can only produce positive values, because all independent variables are raised to a power and multiplied by positive numbers. In all functions, diameter at breast height is used as an independent variable. Tree height is used in the equations describing the biomass of stem wood, biomass of stem bark of pine and birch, biomass of stem over bark of spruce, and biomass of dead branches of birch. In addition to diameter at breast height, either crown limit or relative height of a tree is used as an independent variable in all of the models for biomass of different crown components of pine and in a model for the biomass of living branches of birch.

3.1.5 Models selected for the further evaluation

Marklund's (1988) and Hakkila's (1972a, 1979, 1991) models were selected for closer consideration on the basis of data used for the formulation of the biomass models, the existence of models for different components of a tree, and the use of independent variables (see Tables 3, 4 and 7). In addition to the breast height diameter, at least tree height has to be included as an independent variable for the biomass models in order to take into account the effects of growing conditions on the biomass of different components of a tree. Thus, Marklund's (1988) models having both breast height diameter and tree height as independent variables were chosen for the further study for all other above-ground components of a tree, ex-

cept for living branches of birch. For this case the model having only breast height diameter as an independent variable was selected (Table 8). Also the models for the biomass of stump and biomass of roots have only breast height diameter as an independent variable.

Table 8. The selected Marklund's (1988) models for the biomass (kg) of trees on mineral soils. The explanations of the symbols for independent variables are represented on the pages 9-10.

Dependent variable	Model
Scots pine	
ln(stem wood)	7.6066*(d/(d+14))+0.02*h+0.8658*ln(h)-2.6864
ln(stem bark)	7.2482*(d/(d+16))+0.4487*ln(h)-3.2765
ln(living branches incl. needles)	13.3955*(d/(d+10))-1.1955*ln(h)-2.5413
ln(needles)	12.1095*(d/(d+7))+0.0413*h-1.565*ln(h)-3.4781
ln(dead branches)	7.1270*(d/(d+10))-0.0465*h+1.1060*ln(h)-5.8926
ln(stump)	11.0481*(d/(d+15))-3.9657
ln(roots ≥ 5 cm)	13.2902*(d/(d+9))-6.3413
ln(roots < 5 cm)	8.8795*(d/(d+10))-3.8375
Norway spruce	
ln(stem wood)	7.2309*(d/(d+14))+0.0355*h+0.703*ln(h)-2.3032
ln(stem bark)	8.3089*(d/(d+15))+0.0147*h+0.2295*ln(h)-3.402
ln(living branches incl. needles)	10.9708*(d/(d+13))-0.0124*h-0.4923*ln(h)-1.2063
ln(needles)	9.7809*(d/(d+12))-0.4873*ln(h)-1.8551
ln(dead branches)	3.6518*(d/(d+18))+0.0493*h+1.0129*ln(h)-4.6351)
ln(stump)	10.6686*(d/(d+17))-3.3645
ln(roots ≥ 5 cm)	13.3703*(d/(d+8))-6.3851
ln(roots < 5 cm)	7.6283*(d/(d+12))-2.5706
Silver and downy birch	
ln(stem wood)	8.1184*(d/(d+11))+0.9783*ln(h)-3.3045
ln(stem bark)	8.3019*(d/(d+14))+0.7433*ln(h)-4.0778
ln(living branches excl. leaves)	10.2806*(d/(d+10))-3.3633
ln(dead branches)	11.2872*(d/(d+30))-0.3081*h+2.6821*ln(h)-6.6237

From Hakkila's (1972a, 1979, 1991) biomass models it was not possible to get a full set having the same independent variables. The combination of Hakkila's (1991) models describing the biomass of crown components and having diameter at breast height, height or crown ratio as independent variables were selected for more detailed study (Table 9). Comparability with selected Marklund's (1988) models was applied as a criterion in the selection of Hakkila's (1972a, 1979, 1991) models.

Finér's (1989, 1991) and Laiho's (1997) models for the biomass of different components of a tree are based on the variables determined from small numbers of trees growing on individual peatland stands, and therefore their applicability is very limited. However, the analysis of these models gives valuable information about the application of mineral soil models on peatlands. Although the models cannot describe all the ecosystem behavior, they may be useful for parts of the problem (Mankin et al. 1979). In order to identify the general trend in allocation of biomass to the different components of the trees growing on peatlands, comparisons were

Table 9. The selected Hakkila's (1972a, 1979, 1991) models for the biomass (kg) of trees on mineral soils. In Hakkila's (1991) original functions for the biomass of different components of the crown, the breast height diameter is expressed in mm, and the tree height in dm. Therefore, the variables d and h are multiplied by 10. Hakkila's (1972a) functions for stump and roots were converted into formula, in which breast height diameter was used as an independent variable instead of stump diameter (see Hakkila (1972a)). The explanations of the symbols for the independent variables are represented on the pages 9-10.

Dependent variable	Model
Scots pine	
Stem wood	
2.5 – 7.4 m	$(-27.43*(d/t)^2+62.44*\ln(h/d)-26.88*\ln(h/t)+0.526*h+381.63)* \ 1.01*V_{bl}$
> 7.4 m	$(92.930*(h/d)-193.00*(h/t)^2+1.832* \ (t/h)+341.77)*1.01*V_{bl}$
Stem bark	
2.5 – 7.4 m	$((-27.43*(d/t)^2+62.44*\ln(h/d)-26.88*\ln(h/t)+0.526*h+381.63) *0.99*V)-$
	$((-27.43*(d/t)^2+62.44*\ln(h/d)-26.88*\ln(h/t)+ 0.526*h+381.63)* \ 1.01*V_{bl})$
> 7.4 m	$((92.930* \ (h/d)-193.00*(h/t)^2+1.832* \ (t/h)+341.77)*0.99*V)-$
	$((92.930*(h/d)-193.00* \ (h/t)^2+1.832* \ (t/h)+341.77)*1.01*V_{bl})$
ln(living branches incl. needles)	$3.4914*\ln(d*10)-1.9498*\ln(h*10)-47.454*((d*10)/(h*10)^2)-5.2678$
ln(needles)	$1.8485*\ln(d*10)+0.0155*cr-9.01$
Dead branches	$0.0194*(d*10)-0.84$
Stump and roots	$0.044*(d/0.7604)^2-4.9$
Norway spruce	
Stem wood	
2.5 – 7.4 m	$(-67.35*\ln(d/t)-0.270*t+0.001679*h^3+ \ 167.7/t-9.837*V^2+ 17.79*(d/t)^3+307.21)* \ 1.01*V_{bl}$
> 7.4 m	$(-67.95*\ln(d/t)-0.2795*t+0.619*h+19.13* \ (d/t)^3+303.37)*1.01*V_{bl}$
Stem bark	
2.5 – 7.4 m	$((-67.35*\ln(d/t)-0.270*t+0.001679*h^3+ \ 167.7/t-9.837*V^2+17.79*(d/t)^3+307.21)* \ 1.01*V)-((-67.35*\ln(d/t)-0.270*t+0.001679*h^3+ \ 167.7/t-9.837*V^2+17.79*(d/t)^3+ 307.21)*1.01*V_{bl})$
> 7.4 m	$((-67.95*\ln(d/t)-0.2795*t+0.619*h+19.13*(d/t)^3+303.37)*1.01*V)-((-67.95*\ln(d/t)-0.2795*t+0.619*h+19.13*(d/t)^3+303.37)*1.01*V_{bl})$
Living branches incl. needles	$0.00026724*(d*10)^2+1.41*10^{-6}*(d*10)^3+0.00043562* \ ((d*10)^3/(h*10))+0.4112$
Needles	$1.592*10^{-8}*(d*10)^3*cr+4.73*10^{-6}*(d*10)*cr^2+0.37$
Dead branches	$0.0134*(d*10)+3.9*10^{-8}*(d*10)^3-0.62$
Stump and roots	$0.060*(d/0.7411)^2-7.1$
Silver and downy birch	
Stem wood	
2.5 – 7.4 m	$(22.84*\ln(t)+2.771*(t/d)+379.99)*1.01*V_{bl}$
> 7.4 m	$(34.156*\ln(t)+138.5/d+335.64)*1.01*V_{bl}$
Stem bark	
2.5 – 7.4 m	$((22.84*\ln(t)+2.771*(t/d)+379.99)*1.015*V)-((22.84*\ln(t)+2.771*(t/d)+379.99)*1.01*V_{bl})$
> 7.4 m	$((34.156*\ln(t)+138.5/d+335.64)*1.015*V)-(34.156*\ln(t)+138.5/d+335.64)*1.01*V_{bl})$
ln(living branches excl. leaves)	$2.73067*\ln(d*10)+1788.90/(h*10)^2+0.01664*cr-12.4606$
Dead branches	$0.0040*(d*10)-0.07$

made for all other peatland models introduced in the Appendices 7 and 8 except Laiho's (1997) model for stem over bark of spruce. Laiho's (1997) model for stem over bark of spruce was excluded from the further comparisons, because the comparisons were made separately for the outputs of the models for stem wood and for the outputs of the models for stem bark.

The number of trees, for which the biomass of the stem wood and stem bark were calculated using Hakkila's (1979) models for the basic density of wood and Laasasenaho's (1982) volume functions, was smaller than the number of trees for which the biomass of other components of trees were estimated (see Appendix 1, 2 and 3). The thickness of bark was not measured for all sample trees in NFI data, and thus, the biomass of stem without bark was not able to be estimated for all trees using Hakkila's (1979) and Laasasenaho's (1982) models. When the comparisons were made between the outputs of Marklund's (1988) and Hakkila's (1979) models for stem wood and stem bark, also this smaller number of trees was used for estimation of the biomass by Marklund's (1988) models. For other components, the biomass was calculated for larger numbers of trees in order to take a wider diameter range into account, and produce more general results.

In order to calculate biomass of different components of a tree, certain corrections and adjustments were made to some models. The error that occurs in the retransformation of logarithmically transformed dependent variable is not taken into account in Hakkila's (1991) and Finér's (1989, 1991) functions. In these functions the correction was made by adding expression $s_{res}^2/2$ (where s_{res} = Residual standard deviation) to the constant (see Finér 1989, Kangas 2001b).

Separate Hakkila's (1979) models were used to estimate the densities of stem wood for trees having height 2.5-7.4 m and for trees >7.4 m. The stem densities of trees having heights <2.5 m was extrapolated using models for trees having heights 2.5-7.4 m. Because Hakkila's (1979) functions illustrate the basic density of knot-free and bark-free stem, the corrections introduced by Hakkila (1979) were taken into account in the calculations of this study. For pine and spruce, the effect of climatic zone on the density of wood was also taken into account. Based on Hakkila's (1979) study the density of pine stems was decreased by 7% when the temperature sum was 500-749 d.d. (degree days), and by 3% when it was 750-869 d.d. In spruce the increase of wood density of stem was 5% when the temperature sum was 750-999 d.d..

Because Hakkila (1972a, 1979, 1991) has no model for the biomass of stem bark, the usability of the difference between biomass of stem over bark and that of stem wood was investigated. The wood densities (with and without bark) are estimated using Hakkila's (1979) models. The biomass of stem over bark and stem wood were estimated by multiplying the wood densities by the stem volumes. The volumes of the stems over the bark and those of stem wood are produced using Laasasenaho's (1982) functions based on diameter at the breast height and tree height, if the heights of pines and spruces are >3 m, and >4 m for birches. In NFI data the volumes of shorter trees are calculated using equations not documented (Kari T. Korhonen, Finnish Forest Research Institute, 2004, personal communication).

Marklund's (1988) and Hakkila's (1991) functions for living branches of pine and spruce also include needles, for which the mass of needles estimated by using

separate functions was subtracted from those functions of living branches. For birch the biomass of leaves could not be included into the calculations because of a lack of models, and therefore the proportions of different components of birch are not fully comparable with those of conifers. Hakkila (1991) and Finér (1989, 1991) used crown ratio as one of the independent variable in some models. It was calculated as relation of height of living crown and the height of a tree. Laiho (1997) used the relative height of a tree as one independent variable in models for living branches of birch and dead branches of pine. The relative height of a tree means the relation between height of a tree and the dominant height of the trees growing in a stand. When these functions were applied in this study, it was assumed, that heights of considered trees correspond to the dominant height, for which the value of the relation was 1.

The biomass estimates of the total above-ground components of a tree was defined as a sum of separately calculated biomass regression functions of the single components. Marklund (1988) and Hakkila (1972a, 1979, 1991) have not formulated functions for the total above-ground components of a tree. Thus, the sums could not be compared with the outputs of the biomass function for the total above-ground biomass of a tree.

According to Marklund's (1988) recommendations, his functions for roots having diameter <5 cm were used for pines and spruces, whose diameters at breast height were <10 cm. The root biomass of thicker trees was calculated as a sum of function for roots having a diameter <5 cm and that for thicker roots. Hakkila's (1972a) biomass functions for stump and roots of pine and spruce have stump diameter as the only independent variable. In this study, the stump diameters were estimated using Hakkila's (1972a) functions, in which breast height diameter was an independent variable.

The studied biomass models did not include seedlings having heights <1.3 m. For the formulation of biomass functions of seedlings <1.3 m tall, diameter at breast height cannot be used as one of the independent variables. The biomass of small seedlings should be modeled separately. However, the problem in using separate functions is the compatibility of the functions. In this study, the biomass of seedlings <1.3 m tall was excluded.

The standard deviations of the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models in the different diameter classes were compared only for stem wood and the sum of above-ground components of pine, spruce and birch, and living branches and needles of pine and spruce. This was because for these components and tree species, both Marklund (1988) and Hakkila (1979, 1991) had models that have other independent variables in addition to breast height diameter. The standard deviations were also compared for stem bark, if the outputs for biomass of stem bark were reasonable.

3.2 Tree-level evaluation with selected models

3.2.1 Results on mineral soils

By tree species

On mineral soils Marklund's (1988) functions for the biomass of stem wood resulted in the largest absolute values for birch, then for spruce, and the smallest ones for pine in diameter classes <40 cm (Figure 4). In most of the larger diameter classes, spruce had a bigger biomass than birch. Hakkila's (1979) model gave the largest absolute values for the stem wood biomass for birch. The biomass estimates of pine and spruce stem wood did not differ much until the diameter at breast height is 30 cm, but for thicker trees the estimates for pine were larger.

The variation of the stem wood biomass estimates between the different tree species was partly a consequence of differences in heights within the same diameter classes. In the NFI data used, birches were taller than conifers in most of the diameter classes (Appendix 9). Among the thinnest trees (≤7 cm), pines were taller than spruces, but otherwise pines were shortest trees. This corresponds well with other studies. For example, according to Hakkila et al. (1972) spruces are a little taller than pines in the same diameter classes. Laasasenaho's (1982) functions gave the largest volumes for stem wood of birches and spruces excluding the trees in the larger diameter classes (Appendix 9). In larger diameter classes, the highest values were for spruce, then pine, and the lowest values were for birch.

According to the outputs of Hakkila's (1979) models, the basic stem wood density is highest in birches, and the basic density of Scots pine is higher than that of Norway spruce (Appendix 9). This is supported by Hakkila's (1966) study. The calculations of wood density using Marklund's (1988) biomass models and Laasasenaho's (1982) volume functions produced the highest wood density for stem wood of birch, but the order of wood densities of pine and spruce varied between diameter classes. This variation was caused by compatibility problems between Marklund's (1988) biomass functions and Laasasenaho's (1982) volume functions (see the section '*By site fertility*' in this chapter). In some studies where there was a rather narrow diameter range, the dry mass of pine stem wood has been reported to be higher than that of spruce (Hakkila 1971), and green mass has been lower in pine than in birch (Hakkila et al. 1975) in the same diameter class. Because the order of average green density of stem wood of the studied tree species is the same as that of basic density (Hakkila 2002), the lower green mass in pine than in birch also means lower dry mass in pine than in birch.

In summary, on average the biomass of stem wood could be assumed to be larger at least in small- and medium-sized birches than in conifers of the same size. The outputs of both Marklund's (1988) and Hakkila's (1979) models corresponded with this conclusion. Even if the models produced small differences in the ranking of spruces and pines in the same diameter classes, no conclusions about the relations of the biomass of stem wood of these tree species cannot confidently be made.

The estimation of the biomass of stem bark proved to be unreasonable when calculated from the difference between biomass of stem over bark and the biomass of stem wood (see the section 'By size of tree' in this chapter). Thus, the ranking of tree species concerning the biomass of stem bark was compared only using the outputs of Marklund's (1988) models. The outputs of Marklund's (1988) models for the biomass of stem bark (Figure 4) corresponded with Hakkila's (1967) previous study. According to Hakkila's (1967) study the biomass of stem bark is the biggest for birch, then spruce, and the lowest for pine, when the stems having same volumes were considered. Olsson (1978) reported similar results. Based on these studies, the biomass of stem bark in the same diameter classes is the highest in birch and the lowest in pine.

The ranking of the biomass estimates for living branches and for the needles of pine and spruce (Figure 4) were coincident with the previous studies – i.e. the estimates for spruce were bigger than those for pine (Hakkila 1969, 1971, 1989). The estimates produced by Marklund's (1988) models for living branches of birch were higher than those of spruce. Excluding the thickest trees (>35 cm), Hakkila's (1991) models gave a larger biomass of living branches for spruce than for birch. In the largest diameter classes the results were the opposite. The comparison of the biomass of living branches between conifers and birch was problematic because of a lack of studies reporting results for this variable. In the used NFI data, the birch crowns were longer than the crowns of pines and spruces in the smallest diameter classes (≤7 cm), but in other diameter classes spruce crowns were the longest and pine crowns were the shortest (Appendix 9). The crown ratio of spruce was the largest in all diameter classes. Excluding the smallest diameter classes, the crown ratio of birch was also generally higher than that of pine for the NFI data. According to a study by Hakkila et al. (1972), on average crown ratio was largest in spruce, and the crown ratio of birch was a little larger than that of pine. The branches of spruce were thinnest and on average the branches of birch were a little thicker than those of pine (Hakkila et al. 1972). Due to the lack of representative studies, the comparisons between the conifers and birch about the amount, length, and basic density of branches were impossible to make.

According to Hakkila (1989), pine has more biomass in dead branches than spruce, and because of poor durability and dead material quickly breaking off, standing birch has a relatively small mass of dead branches compared with the two conifers species. Excluding the thickest trees these results corresponded with the outputs of the studied models (Figure 4). In the largest diameter classes Marklund's (1988) and Hakkila's (1991) models gave higher values for spruce than for pine. Hakkila (1969) reports, especially in these largest diameter classes, that the biomass of dead branches of pine was larger than that of spruce.

Because the biomass of stem bark cannot be estimated as a difference between the biomass of stem over bark and stem wood (see the section 'By size of tree' in this chapter), the biomass of stem over bark (Appendix 5) was used, when the total biomass of above-ground components were estimated using Hakkila's (1979, 1991) models. The summing up of the outputs of the models resulted the smallest biomass estimates for the above-ground components for pine (Figure 4). The biomass estimates of above-ground components of birch were a little higher than that of spruce, but the variation between the larger diameter classes was considerable. The
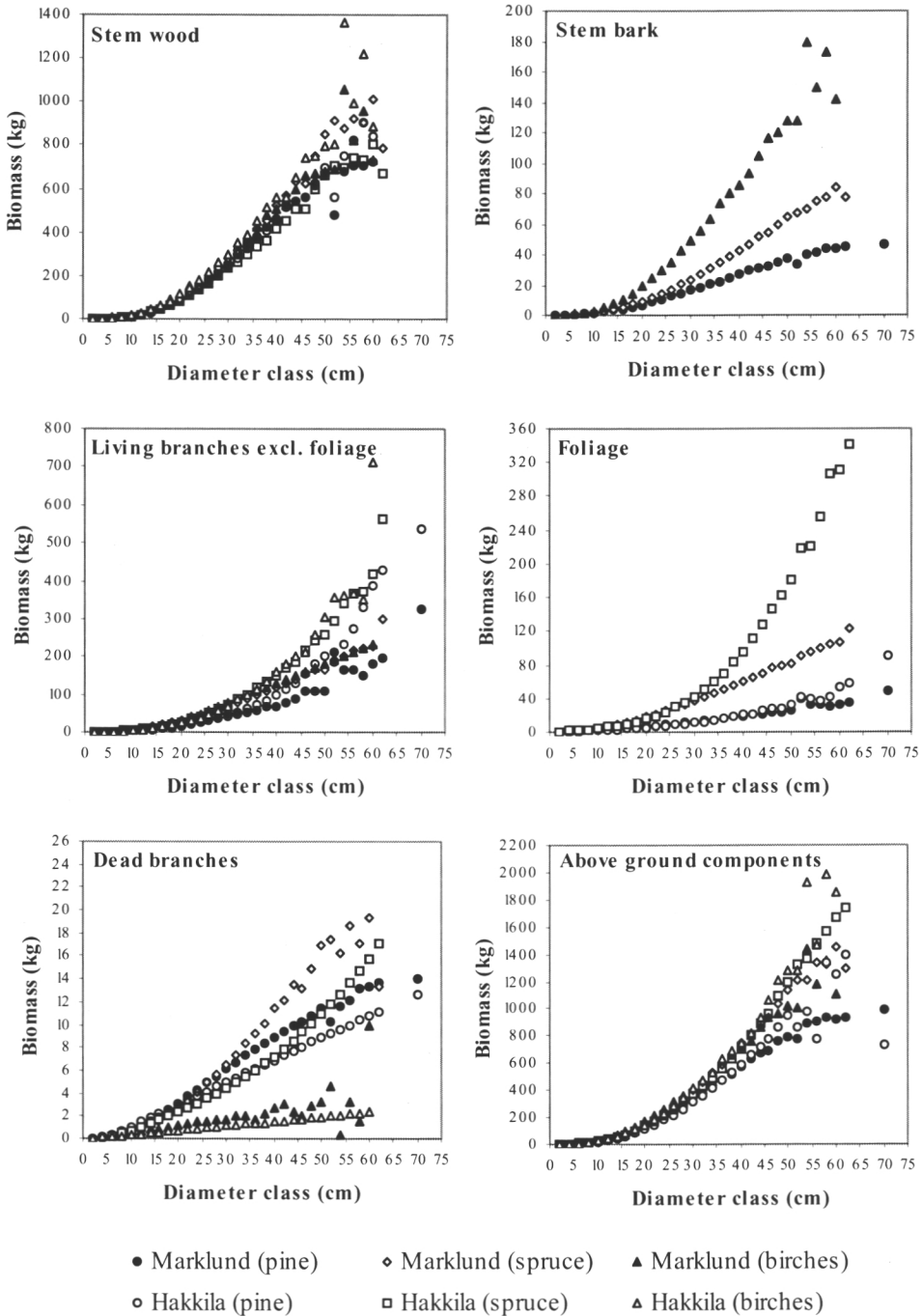
Figure 4. The biomass of single above-ground components of trees and the biomass of the sum of all above-ground components of trees by tree species estimated using Marklund's (1988) and Hakkila's (1979, 1991) models in different diameter classes on mineral soils.

results corresponded with the studies of Hakkila et al. (1978) and Simola (1977), when the green mass of small-sized pines and birches were compared. When the above-ground biomass of trees were estimated using coefficients obtained from Kauppi's et al. (1995) study, and the differences in the volumes and mean basic densities of the stems in different tree species (Hakkila 1966) were taken into account, in most of the diameter classes the biomass of birch was about the same or a little larger than the biomass of spruce, which were larger than those of pine (Appendix 11).

The evaluated Hakkila's (1972a) functions gave larger biomass for the stump and the roots for spruce than for pine (Figure 5). Excluding the trees in the diameter classes >30 cm, Marklund's (1988) models gave nearly parallel results of the biomass of stump for pine and for spruce. In the larger diameter classes, spruce had a larger biomass than pine. For the biomass of roots, Marklund's (1988) models produced larger estimates for spruce than for pine. In Hakkila's (1976) study the biomass of stump-root system was larger for spruce than for pine in diameter classes >22 cm, but in smaller diameter classes the situation was the opposite.
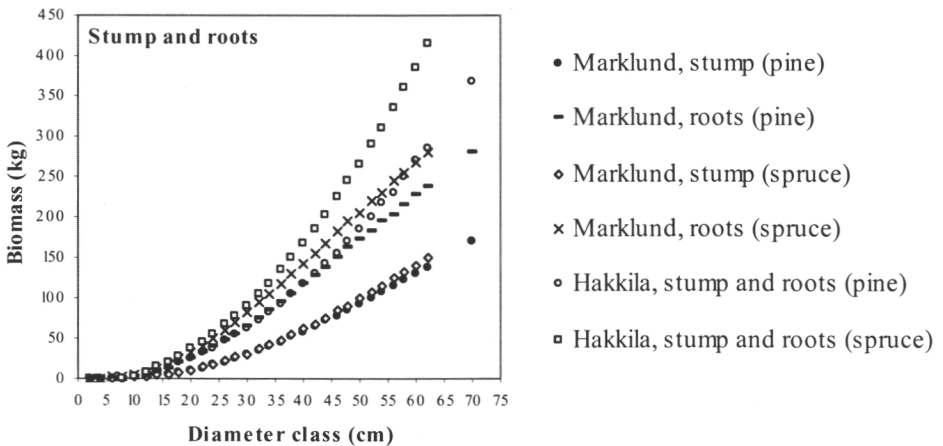
Figure 5. The biomass of stump and roots of pines and spruces estimated using Marklund's (1988) and Hakkila's (1972a) models in different diameter classes on mineral soils.

The allocation of biomass to the different above-ground components of a tree was examined using only Marklund's (1988) models (see the section '*By size of tree*' in this chapter). On mineral soils Marklund's (1988) functions produced the highest proportions of stem wood for birch in the smaller and some of larger diameter classes, but otherwise the proportions were highest for pine and smallest for spruce (compare Table 10). When the relations between the outputs of Marklund's (1988) models were considered, the percentage of stem bark from the biomass of above-ground components of a tree was highest for birch. In the smaller diameter

classes the percentage was larger in pine than in spruce. For the larger diameter classes the percentage was larger in spruce than in pine. When the biomass of living branches was estimated using Marklund's (1988) models, the relative shares of living branches of pine were generally smaller than those of spruce and birch. The proportions of living branches were the biggest in spruce in the smaller diameter classes and some larger diameter classes, but in most of the classes the percentages were highest in birch. The proportion of needles from the above-ground biomass was bigger in spruce than in pine. When the results of Marklund's (1988) models were considered, the percentage of dead branches was the largest in pine and the smallest in birch. When the different tree species were studied, it was difficult to compare the relative shares calculated based on outputs of Marklund's (1988) models with previous studies. The information collected from literature about the percentages of different components was very restricted (see the section 'By size of tree' in this chapter).

By size of tree

Marklund's (1988) functions behaved logically for most of the diameter classes. Due to their formula they did not produce negative values of biomass for any tree components. Most of Hakkila's (1972a, 1979, 1991) models produced reasonable results within the range of the material used for formulating the models; however, extrapolation was not possible using most of the models. In a few diameter classes (e.g. 52 cm and 70 cm in pine, 62 cm in spruce, and 54 cm and 58 cm in birch) some Marklund's (1988) and Hakkila's (1979, 1991) models gave exceptionally high or exceptionally low estimates (Figure 4) because of larger or smaller average heights than in neighboring diameter classes (Appendix 9). The unusual combinations of mean breast height diameter and tree height were caused by small amount of sample trees in these diameter classes. The study of biomass estimated for single trees in the used NFI data revealed similar results about the exceptional biomass estimates as the study of mean biomass in different diameter classes.

The largest differences between the outputs of Marklund's (1988) and Hakkila's (1979) models for the biomass of stem wood could be seen outside the range of sample tree data used for the construction of Hakkila's (1979) models. Excluding the smallest and largest diameter classes, the differences between the outputs of the models in the biomass of stem wood of all studied tree species were smaller than 20% (Figure 6). Excluding only a few of the smallest and largest diameter classes, the differences in the standard deviations of the biomass of stem wood of pine were also less than 20% within the diameter classes (Figure 7). For spruce the differences in the standard deviations within the diameter classes were rather small within a wide range of diameter classes, but in birch this was only the case for a narrow range of middle-sized diameter classes (4-22 cm).

The difference between Laasasenaho's (1982) volume functions for stem over bark and stem wood could not be used for the estimation of the volume of stem bark, because the volume functions produced unrealistic values in relation to each other in many diameter classes, especially in the smallest and some of the larger diameter classes. Thus, it was not possible to estimate the biomass of stem bark as

a difference between the biomass of stem over bark and that of stem wood, when the volume was estimated using Laasasenaho's (1982) functions and the basic density was determined using Hakkila's (1979) functions.

The outputs of Marklund's (1988) biomass models for living branches and those for needles of pine and spruce differed by more than 20% from Hakkila's (1991) models for the smaller and the larger diameter classes (Figure 6). However, excluding the living branches of spruce, the differences in the standard deviations were high within most of the diameter classes (Figure 7). The differences in the standard deviations of the biomass estimates of living branches of spruce were less than 20% in diameter classes representing middle-sized trees (13-44 cm). Hakkila's (1991) models for living branches of all studied tree species and the model for needles of spruce resulted in an unreasonably high biomass estimates for the thickest trees (Figure 4). Using Hakkila's (1991) models, subtractions of the biomass estimates of needles from the biomass estimates of living branches including needles produced negative values for some pines and spruces in many diameter classes. The difference became negative if short or thin trees were considered. For the living branches of small- and medium-sized birches Marklund's (1988) model gave larger biomass estimates than Hakkila's (1991) model. When the thickest trees were considered, the situation was vice versa (Figure 6). Hakkila's (1991) model for the biomass of living branches of birch could not be used for the shortest trees (≤2 m), because the estimates it produced for these trees were unreasonable high.

For pine and spruce the differences between Marklund's (1988) and Hakkila's (1991) models in biomass estimates of living branches could be linked with the structure of the modeling material. Therefore, Hakkila's (1991) model, derived from more suppressed trees, produced a smaller biomass for the living branches of thin trees. For birch the number of sample trees that had been used for the formulation of the functions is much smaller than the number of sample trees for spruce and pine in both studies (Table 1), and they did not necessarily represent the whole birch population.

Hakkila's (1991) models resulted in negative estimates for dead branches of pine having a breast height diameter of ≤4.3 cm, and for dead branches of spruce having a diameter ≤4.5 cm. Also the biomass of dead branches of the thinnest birches (0-1.7 cm) were negative. The differences in the outputs of Marklund's (1988) and Hakkila's (1991) models for the biomass of dead branches of pine were less than 20% in diameter classes 16-32 cm (Figure 6). Only in a very narrow diameter range did the biomass of dead branches of spruce estimated with Marklund's (1988) model differ less than 20% from the outputs of Hakkila's (1991) model. Both of the examined models for the biomass of dead branches of birch resulted in very low biomass in all diameter classes (Figure 4). Excluding the smallest diameter classes, the estimates for the biomass of dead branches of birch produced by Marklund's (1988) models were generally more than 20% larger than the results of Hakkila's (1991) models. For thin pines and spruces the larger biomass of dead branches estimated by Hakkila's (1991) models could be caused by the biased data. Another explanation is that the prediction of biomass of dead branches is difficult using conventional tree- and stand-level variables (e.g. Hakkila 1991, Petersson 1999). This explanation is indicated by the lower values of multi-
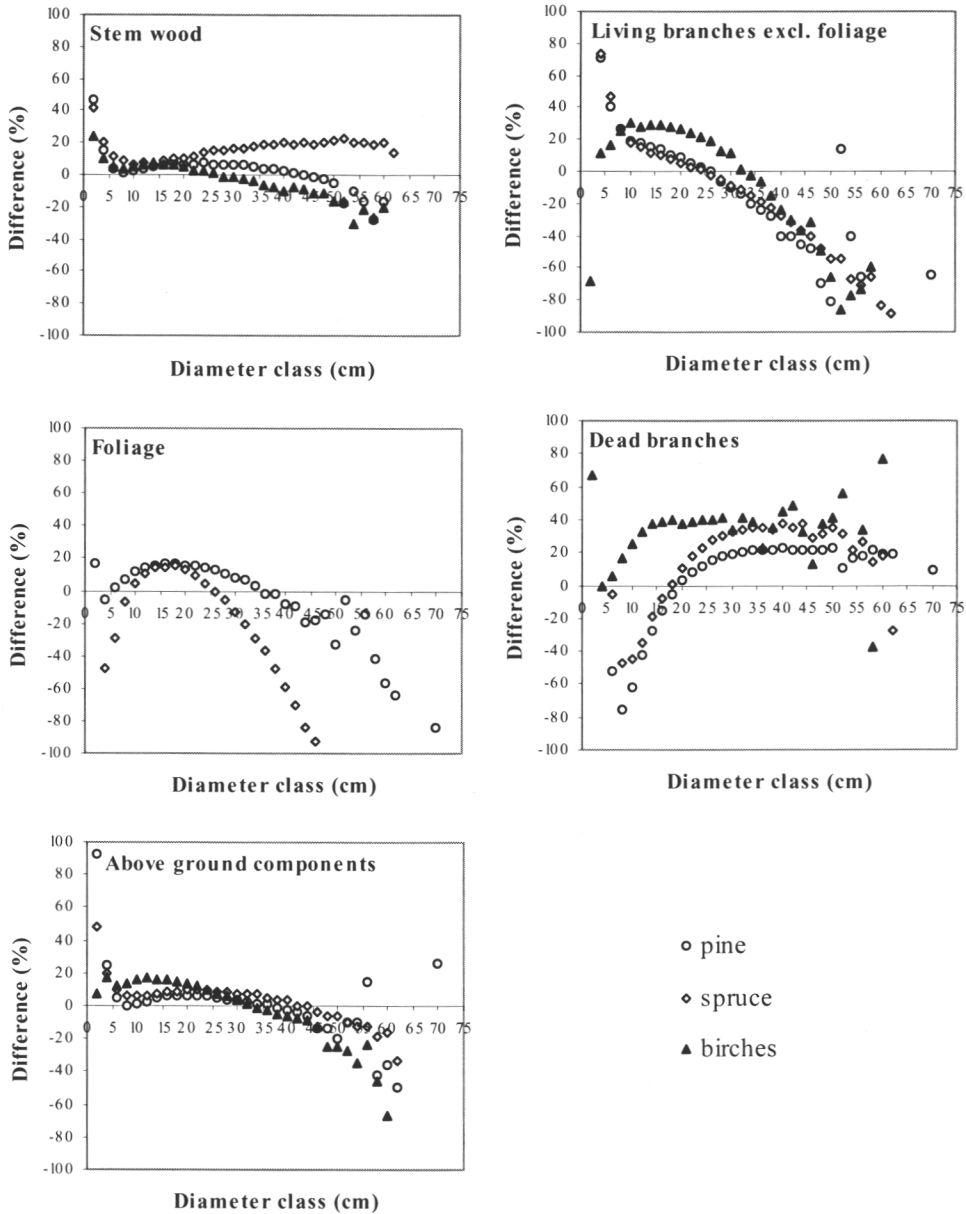
Figure 6. The relative differences in the biomass of single above-ground components of trees and in the biomass of the sum of all above-ground components of trees estimated using Marklund's (1988) and Hakkila's (1979, 1991) models on mineral soils. The positive values mean that Marklund's (1988) models produced higher values than Hakkila's (1979, 1991) models, and the negative values mean that Marklund's (1988) models produced lower values than Hakkila's (1979, 1991) models. In the charts the differences were limited to ±100%.

○ pine   ◇ spruce   ▲ birches
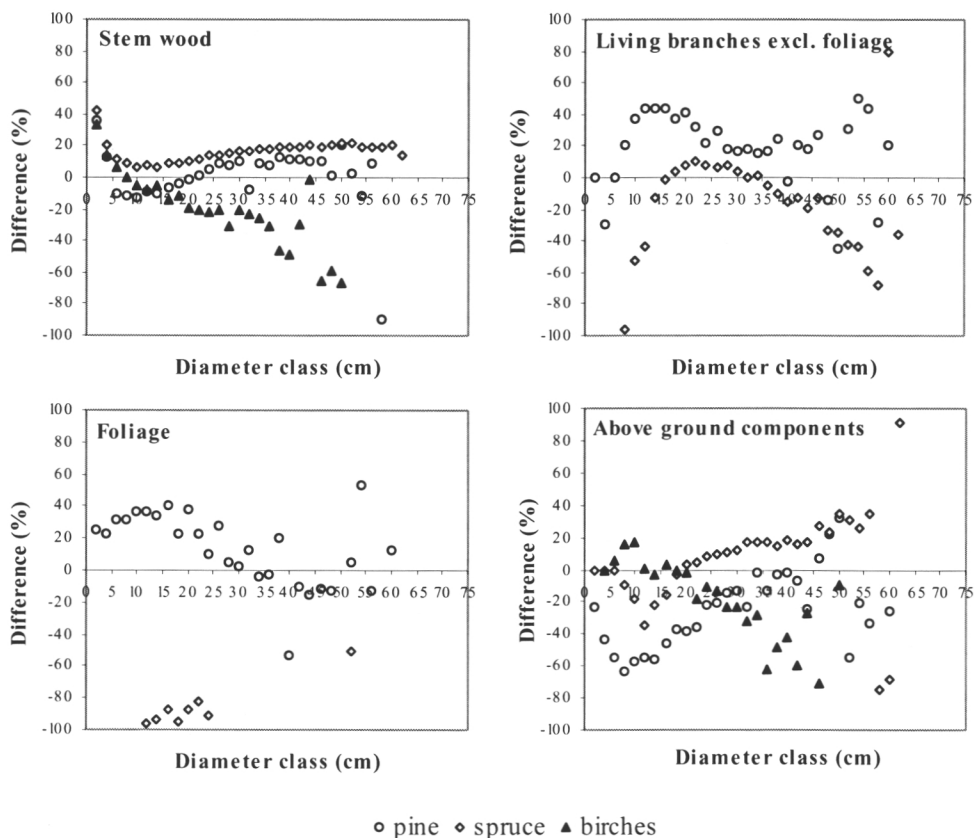
Figure 7. The relative differences between the standard deviations of the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models in different diameter classes on mineral soils. The positive values mean that the standard deviations of the outputs of Marklund's (1988) models were higher than those of Hakkila's (1979, 1991) models, and the negative values mean that the standard deviations of the outputs of Marklund's (1988) models were lower than those of Hakkila's (1979, 1991) models. In the charts the differences were limited to ±100%.

ple correlation coefficient (R), coefficient of determination (R^2) and the high values of residual standard deviation (s_{res}) concerning the biomass models for dead branches compared to the models for other components of a tree (Appendices 4 and 5).

The sum of different above-ground components estimated using Marklund's (1988) models corresponded well with the sum of Hakkila's (1979, 1991) models for a wide diameter range (Figure 6). For pine, there were large differences in the standard deviations of the biomass estimates of the above-ground components of a tree within most of the diameter classes. Excluding some small and the largest diameter classes of spruce and excluding the large diameter class of birch, there were small differences in the standard deviations of the biomass of the above-ground

components of a tree between the outputs of the models (Figure 7). The biomass of stem wood has the largest effect on the total biomass of the above-ground components, and thus, the correspondence of the models in estimating the total biomass of above-ground components depends considerably on their correspondence in estimating the biomass of stem wood.

The dry mass of stumps and roots of pine and spruce was bigger when they were calculated using Marklund's (1988) models (Figure 5). This was because Hakkila (1972a) included only the roots thicker than 5 cm in his data (see chapter 3.1.3). Hakkila's (1972a) model for the biomass of stump and roots produced negative values for pines and spruces having a diameter at breast height ≤8.0 cm.

Because the biomass of bark could not be estimated using Hakkila's (1979) and Laasasenaho's (1982) models and because Hakkila's (1972a, 1979, 1991) models produced unreasonable values for some diameter classes, the proportion of the biomass of the different components of a tree were only calculated using Marklund's (1988) models. In other studies the proportion of stem wood of pine in small-sized trees and in trees in the thinning phase was 30-70%, that of bark 10-15% (Paavilainen 1980, Voipio and Laakso 1992, Vanninen et al. 1996), that of living branches excluding needles 10-35% and that of needles 5-30% (Paavilainen 1980, Voipio and Laakso 1992, Vanninen et al. 1996, Mäkelä and Vanninen 1998). In Hakkila's (1972b) study the percentage of the biomass of stem over bark for middle-sized trees was 60-85% and that of living branches including needles 15-40%. Nylinder (1980) presented very similar results to Hakkila's (1972b) study. The percentages for small- and middle-sized trees obtained using Marklund's (1988) models corresponded with these studies (Table 10). When larger pines were considered, the proportions given by Marklund's (1988) models were also rather similar to other studies. According to Vanninen et al. (1996) the percentages for the biomass of stem wood of large pines were 60-80% and for stem bark 5-15%. In large pines the proportions of living branches excluding needles were 5-20% and those of needles 1-10% according to Vanninen et al. (1996) and Mäkelä and Vanninen (1998). In Nylinder (1980) the proportions of stem over bark varied from 75% to 80%, and those of living branches including needles from 20% to 25%.

Table 10. The range of proportions (%) of different components of trees growing on mineral soils from the total biomass of above-ground components in diameter classes 1-20 cm, 21-40 cm and >40 cm. The biomass of the components was estimated using Marklund's (1988) models.

	Scots pine			Norway spruce			Silver and downy birch		
	1-20 cm	21-40 cm	> 40 cm	1-20 cm	21-40 cm	> 40 cm	1-20 cm	21-40 cm	> 40 cm
Stem wood	51-70	71-78	56-86	30-60	61-68	59-77	53-68	68-70	62-73
Stem bark	6-18	5-6	4-5	6-8	6	5-6	11-17	11-12	12-13
Living branches (excl. foliage)	14-17	13-15	7-33	20-29	16-20	11-24	20-27	18-20	14-23
Foliage	6-15	3-6	2-6	12-31	8-12	5-10			
Dead branches	2-4	2-3	1-2	2-3	1-2	1-2	1-4	0-1	0-2

According to Voipio and Laakso (1992) the proportion of stem wood is about 45%, and that of bark 10% of the above-ground biomass of small-sized spruces. The proportion of branches excluding needles is about 35%, and that of needles about 10%. The proportions obtained from Hakkila's (1972b) study for the biomass of the stem over bark were 50-70%, and for branches including needles 30-50%. When the biomass of stem wood, bark and needles were considered, the estimated proportions obtained using Marklund's (1988) models were rather similar to these studies; however, the percentages of living branches calculated with Marklund's (1988) models were smaller (Table 10) than the percentage obtained by Voipio and Laakso (1992). Nylinder's (1980) comparisons of different biomass studies gave values of about 50-75% for the biomass of stems over bark for trees having a diameter ≤20 cm and about 70-75% for the stems of larger trees. Correspondingly, the percentages of branches including needles were 25-50% in the smaller diameter classes, and 25-30% in the larger ones. Marklund's (1988) models gave similar results.

For birch the percentages of the outputs of evaluated models were also generally similar to the values reported in other studies. One exception was the proportion of stem wood in small birches, for which Marklund's (1988) models gave slightly smaller values (Table 10). The proportions of stem wood in small-sized birches were about 60-85%, and that of stem bark about 10-15% (Björklund and Ferm 1982, Mälkönen and Saarsalmi 1982, Voipio and Laakso 1992). Ferm and Kaunisto (1983) and Ferm (1990) reported that for small birches the proportions of the biomass of stem over bark were about 75-85%. The percentages of living branches without leaves are 10-25% (Simola 1977, Björklund and Ferm 1982, Mälkönen and Saarsalmi 1982, Ferm and Kaunisto 1983, Ferm 1990, Voipio and Laakso 1992) and that of leaves 5-10% (Simola 1977, Mälkönen and Saarsalmi 1982). In a 40-year-old birch stand the proportions of stem wood were 65-75%, those of bark 10-15%, those of branches excluding foliage 10-20%, and those of foliage 5% of the above-ground biomass of the trees (Mälkönen 1977, Mälkönen and Saarsalmi 1982). In Mälkönen (1977) and Mälkönen and Saarsalmi (1982) the proportions of dead branches were 1% at the most. In a dense stand Björklund and Ferm (1982) reported a value of 6% for the biomass of dead branches.

By site fertility

When the biomass of stem wood of pines, spruces and birches growing on various sites was studied, the models generally produced higher values for trees growing on fertile than on infertile sites (Figure 8). In the NFI data used, trees in the same diameter class were taller on the fertile than on the infertile sites (Appendix 10) (see also Ilvessalo 1969, Koivisto 1972, Vuokila and Väliaho 1980), and therefore, the biomass of a stem could be assumed to be larger on fertile sites. According to Päivinen (1978) the pines and spruces growing on fertile sites taper more than those growing on infertile sites. This is supported by Hocker (1979), who states that the stems of trees with long spreading crowns taper more than those with narrow crowns. For birch the site has proved to have no significant effect on the tapering of the stem (Päivinen 1978). In the NFI data used in this study, in the same

diameter classes volumes of stem wood of all studied tree species were larger on fertile than on infertile sites when they were estimated by Laasasenaho's (1982) models (Appendix 10). Thus, for all examined tree species height had a greater effect on stem volume, than taper had on stem volume.

The increase in the tree growth rate decreases the basic density of the wood of pine and spruce (Hakkila 1966, Kärkkäinen 1985); therefore, on the fertile mineral soils the density of wood is less than on infertile sites. For birch, the effect of growth rate on the wood density is generally considered to be insignificant (Hakkila 1966, Kärkkäinen 1985). Trees of a particular diameter are older on infertile sites, than trees of the same diameter growing on fertile sites. Due to – among other things – the changes in the composition and the proportion of heartwood (Kärkkäinen 1985), the density of stem wood increases as trees get older (Hakkila and Uusvaara 1968, Björklund and Ferm 1982, Kärkkäinen 1985, Vanninen et al. 1996). The direction of the change in the basic densities of stems estimated by Hakkila's (1979) functions for trees growing on different site fertilities (Appendix 10) corresponded with results reported in the literature. The relationships between Marklund's (1988) biomass functions and Laasasenaho's (1982) volume functions gave lower basic densities for trees growing on infertile sites in many diameter classes (Appendix 10). This result indicated the poor compatibility of these functions. However, according to preliminary comparisons made in this study the effect of lower wood density was not as great as the influence of larger volume on the biomass of stem wood on fertile sites. Based on these analyses, the biomass of stem wood is larger on fertile than on infertile sites.

Marklund's (1988) models for the biomass of stem bark produced higher estimates on fertile than on infertile mineral soils (Figure 8). According to previous studies the thickness of stem bark of all considered tree species (Östlin 1963b, Päivinen 1978) and the percentages of bark volume of pine and spruce (Östlin 1963b, Ilvessalo 1969, Heiskanen and Rikkonen 1976) were larger on infertile than on fertile sites. However, according to Hakkila (1967) the volume of stem over bark explained most of the variation in the biomass of stem bark. In Hakkila's (1967) study the correlation between the volume of stem over bark and the biomass of stem bark was positive. In that study, the correlation between the biomass of stem bark and growth rate was negative for pine, but the explained variance did not increase much when the growth rate was added into a regression function in addition to volume of stem over bark. Age was positively correlated with the biomass of stem bark of spruce, and height growth rate was negatively correlated with the biomass of stem bark of birch. However, age of spruce and height growth rate of birch had only minor effects on the biomass of stem bark of these tree species in comparison to the effect of stem volume on the biomass of stem bark. Because in the NFI data the volume estimates of trees was larger in the same diameter classes on fertile sites (Appendix 10), the biomass of stem bark could be assumed to be larger on the fertile than on infertile sites, which corresponded with studied Marklund's (1988) models.

The outputs of the models for the biomass of living branches and needles of pine and spruce were contradictory to the results reported in other studies. Marklund's (1988) and Hakkila's (1991) functions produced larger values for biomass of living branches and biomass of needles on infertile than on fertile mineral soils

(Figure 8). The considered Marklund's (1988) model for living branches of birch produced the same result on different sites because it only has breast height diameter as an independent variable. In most of the diameter classes Hakkila's (1991) biomass model for the living branches of birch produced only slight differences between the sites. It generally produced higher values for biomass of living branches of birch on infertile than on fertile sites.

The branches of pine have been studied more extensively than those of spruce and birch. In a study concerning pine, the first whorl of branches from the ground were higher on infertile than on fertile sites (Uusvaara 1983). Based on the results of that study and because in the NFI data the trees were taller on fertile sites, the length of crown can be supposed to be larger on fertile sites (Appendix 10). In some studies the crowns of pines were found to be relatively longer on infertile than on fertile sites (Lämsä et al. 1990, Kellomäki et al. 1992). The results about longer crowns on fertile than on infertile sites were supported by the NFI data (Appendix 10). Generally, in the same diameter classes the crowns of all tree species were longer and the crown ratios were higher on fertile than on infertile sites. In Mäkelä et al. (2000) the biomass of living branches and needles of pine increased exponentially, when the length of crown increases. In that study, the amount of needles and branches was greater for thick-butted trees than for slender trees irrespective of the length of crown.

When pine is considered, the number of branches in a whorl (Lämsä et al. 1990, Kellomäki et al. 1992), the thickness (Hakkila 1971, Turkia and Kellomäki 1987, Kellomäki et al. 1992) and the length of branches are larger on a fertile site than on an infertile site (Hakkila 1971). In contrast to the results for pine, in Heiskanen (1957) there were no large differences in the thickness of branches of birch between different sites on mineral soils. The results for differences in the length of branches of pine were also supported by Valinger (1993), in which fertilization with nitrogen caused greater elongation of branches of pine compared to unfertilized control trees. According to Kellomäki et al. (1992) the total amount of branches of pine is greater on infertile sites. In Hakkila's (1969, 1971) studies, in a certain diameter class, pines and spruces having sharply tapering stems are found to be branchy, and thus, pines and spruces growing on fertile sites have more branches, which is a contradictory conclusion to Kellomäki et al. (1992). According to Kellomäki et al. (1992) the branch biomass of pine is larger on fertile sites than on infertile sites when the stand density is considered as constant. The biomass of branches of birch has been observed to increase, when, for example, the amount of nitrogen (Ferm and Kaunisto 1983, Saarsalmi et al. 1992) and the pH-value of the soil increased (Ferm and Kaunisto 1983). According to Kärkkäinen (1985) the biomass of branches and foliage are large in fast-growing trees because the branchiness of the tree is one of the requirements of its good growth.

In Niinemets et al. (2001) the length, thickness and width of pine needles were generally lower on an infertile than on a fertile site. The needle litterfall of pine has found to be larger on fertile than on infertile sites (Albrektson 1988), which was due to the fact, that a fertile site produces more needles than an infertile one (Bray and Gorham 1964). According to Vanninen et al. (1996) the main difference between an infertile and a fertile site is that the trees on the less fertile site can support more foliage per unit sapwood area.

The outputs of Hakkila's (1991) models for biomass of dead branches did not differ in the same diameter classes on different sites, because the models had only breast height diameter as an independent variable (Figure 8). Marklund's (1988) model for dead branches of pine produced also biomass estimates of same magnitude for all sites, although it had both breast height diameter and tree height as independent variables. For dead branches of spruce Marklund's (1988) function resulted larger values on fertile than on infertile sites and for dead branches of birch they produced higher values on infertile than on fertile mineral soils. According to literature, there are differences in time of formation, amount, dimensions and self-pruning of dead branches on different sites. For example, dead branches of pine are formed earlier (Lämsä et al. 1990) and their amount is greater on fertile than on infertile sites (Kellomäki et al. 1992). In pine, the diameter of the thickest dead branch of a tree increases as site fertility increases (Lämsä et al. 1990). The growing conditions for fungi, bacteria and other micro-organisms have effects on the biomass of dead branches (Petersson 1999). Thus, on fertile sites the self- pruning of pines is faster than on infertile sites (Lämsä et al. 1990). Based on a survey of the literature, no conclusions can be made about the performance of the studied biomass models for dead branches on different site fertilities.

The sums of the biomass for all above-ground components for the evaluated models produced larger biomass estimates for all considered tree species on fertile than on infertile sites. This result was supported by the outputs of Korhonen and Maltamo's (1990) biomass function for the above-ground components of pine (Appendix 11). The main factor affecting above-ground biomass was the biomass of stem wood, and the biomass of stem wood was greater on fertile than on infertile sites.

The outputs of examined models for the biomass of stump and roots were the same irrespective of site fertility, because the models only had breast height diameter as an independent variable. According to the literature there are, however, differences in the biomass of roots depending on the site fertility. The differences in root biomass between site fertilities depended on the classification of the roots, and thus, the results of previous studies differ from each other. According to Vanninen et al. (1996), the relative amount of below-ground section of pines (ages 18-212 years) does not differ much between site types, and therefore, the absolute biomass of roots can be assumed to be larger on fertile sites. In Pietikäinen et al. (1999) the amount of total root biomass did not differ across the moisture gradient on mature (about 100-year-old) conifer stands. In that study the root biomass included living root (tree roots ≤2 mm, tree roots >2 mm, and dwarf shrub roots) and dead root biomass. According to Hynynen (1987) the size of the root system increases as site fertility decreases and as the mechanical hindrances in the soil become less. In Mäkelä et al. (2000) the density of fine roots (<2 mm) of pine was greater in infertile than in fertile sites. There are only a very few studies about the biomass of roots of spruce (e.g. Hakkila 1972a, 1976) and no representative studies could be found concerning the effect of site fertility on the root biomass of birch.

According to the outputs of the studied Marklund's (1988) functions, the percentage of stem wood was generally greater on fertile than on infertile mineral soils for all tree species. The percentage of living branches of all species was
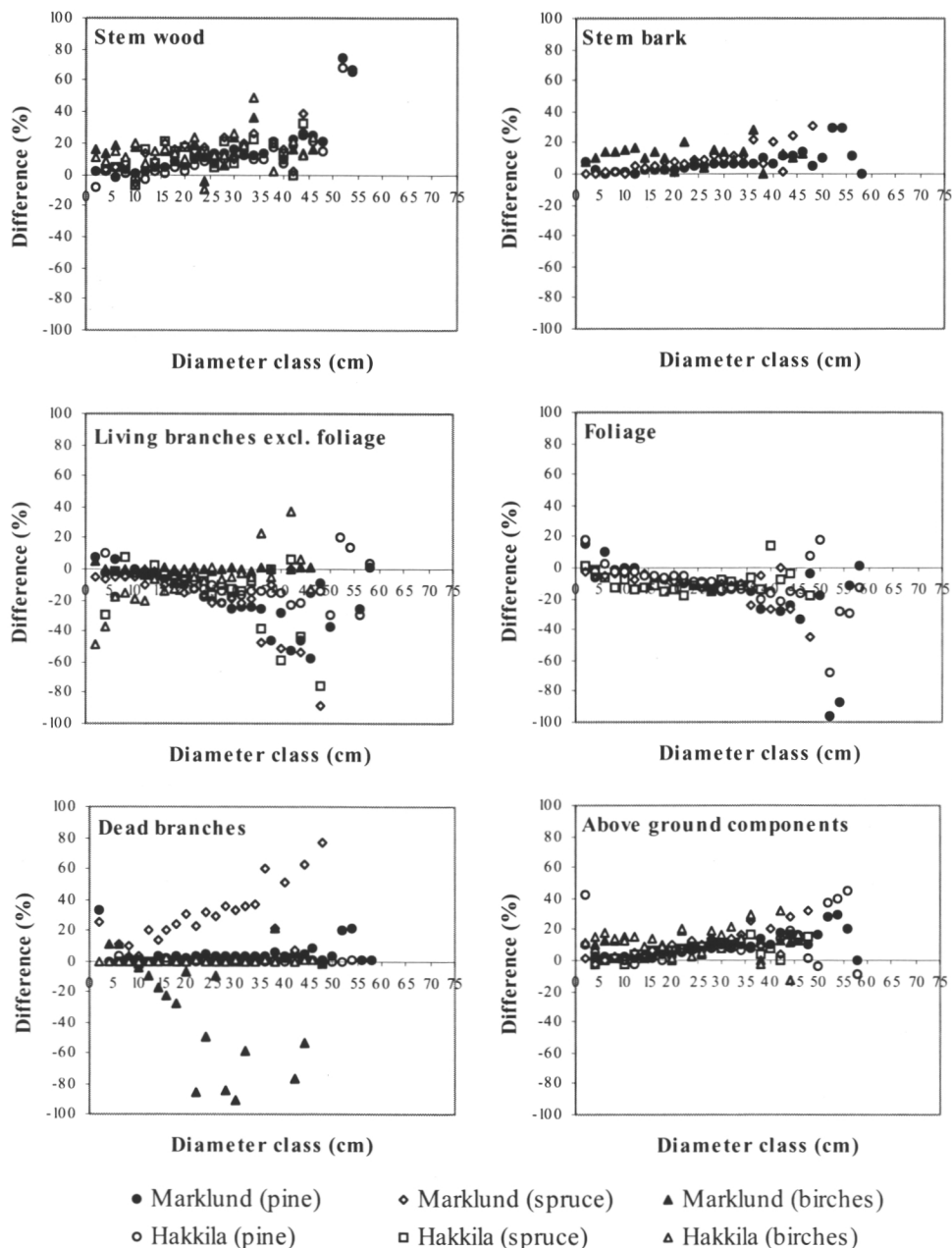
Figure 8. The relative differences in the biomass of single above-ground components of trees and in the biomass of the sum of all above-ground components of trees estimated using Marklund's (1988) and Hakkila's (1979, 1991) models on fertile and on infertile sites. The positive values mean that the biomass estimates were higher on fertile sites, and the negative values mean that biomass estimates were higher on infertile sites. In the charts the differences were limited to ±100%.

greater on infertile than on fertile mineral soils, and for pine and spruce the percentage of needles was greater on infertile than on fertile mineral soils. The site did not have much effect on the relative shares of stem bark and dead branches. Because of the lack of existing studies, the results about the relative proportions of different above-ground components could be compared only with single studies. According to Hakkila (1969), in short trees the relative branch mass is high, and therefore, on infertile sites the proportion of branch mass is higher than on fertile sites. However, according to Kellomäki and Väisänen (1986), the percentage of branch mass of pine is smaller on an infertile than on a fertile site, which is the opposite result to that obtained with the Marklund (1988) models.

By location

Marklund's (1988) and Hakkila's (1979) models produced lower estimates for trees in Northern Finland than in Southern Finland (Figure 9). According to Hakkila (1971) and Hakkila et al. (1972) the trees of a certain diameter class growing in the North were shorter than trees of the same diameter class growing in the South. These kinds of differences in the heights of the trees having same diameters were also noticed in the NFI data (Appendix 12). With regard to the tapering of a stem, there were contradictory results. According to Päivinen (1978) the stem tapering for pine is greater in Southern than in Northern Finland, but according to Hakkila (1971, 1972a) and Hakkila et al. (1972) northern pines taper more than southern ones. According to Päivinen (1978) there are little differences in tapering of spruce in different parts of the country. In Hakkila et al. (1972) the tapering of stems of spruces and birches was observed to be greater in the North. For birch, Päivinen (1978) reports that tapering is greater in the South. Generally, in the same diameter classes the volumes of stem wood estimated by Laasasenaho's (1982) functions were larger in Southern than in Northern Finland in the NFI data (Appendix 12).

Also, the wood density depends on the location. According to Hakkila (1968), in Finland the basic density of, for example, pine and spruce pulpwood is highest in the area between 64°N and 66°N. In that study, pine pulpwood was exceptionally low in density in Northern Finland. In spruce the variation of basic density of wood from the North to the South was relatively small. Hakkila's (1979) models resulted in slightly higher stem wood density estimates for trees growing in Northern than in Southern Finland (Appendix 12). The relations between the outputs of Marklund's (1988) biomass models and those of Laasasenaho's (1982) volume functions produced higher stem wood density estimates for pine in the South than in the North. The stem wood density estimates for spruce and for birch produced by those relations were rather similar in different locations. In summary, the biomass of stem wood of all tree species could be assumed to be larger in Southern than in Northern Finland, because the stem volumes were larger in the South than in the North, and there were rather small differences in basic densities in different parts of Finland.

The outputs of Marklund's (1988) models describing the biomass of stem bark were coincident with other studies. Marklund's (1988) models gave smaller estimates in Northern than in Southern Finland (Figure 9). For pine, the thickness of

stem bark (Östlin 1963a and 1963b, Ilvessalo 1965) and the dry mass of stem bark per stem volume over bark (kg/m^3) (Olsson 1978) were smaller in the North than in the South. For spruce, the results concerning the variation of thickness of stem bark (Östlin 1963a, Ilvessalo 1965, Päivinen 1978) in different parts of Sweden and Finland, and concerning the biomass of stem bark per tree volume (Olsson 1978) in different parts of Sweden were contradictory to those of pine. According to Östlin (1963a) the bark of birch is thicker in Southern than in Northern Sweden; this is affected by the occurrence of different birch species in the different parts of the country. Because, according to the NFI data, the volumes of stems of all considered tree species were smaller (Appendix 12), and because, according to Östlin (1963b), the volume percentage of stem bark of pine and birch was on the average smaller in the North than in the South, at least the volume of stem bark of pine and birch is larger in Southern than in Northern Finland. In Östlin (1963b) the mean volume percentage of stem bark of spruce from the volume of stem over bark was only a little larger in Northern than in Southern Sweden, and thus, also the volume of stem bark of spruce could be assumed to be larger in Southern than in Northern Finland.

For living branches of pine and spruce the considered models resulted in larger biomass estimates in Northern than in Southern Finland (Figure 9). For living branches of birch, Hakkila's (1991) model resulted in smaller biomass estimates on mineral soils in Northern than in Southern Finland, and Marklund's (1988) model resulted in similar biomass estimates in the different parts of Finland, because it has only breast height diameter as an independent variable. In the NFI data, the crowns of all tree species were longer in Southern than in Northern Finland, when same diameter classes were compared (Appendix 12). According to previous studies the crown ratios of pine and spruce are larger in Northern than in Southern Finland (Hakkila et al. 1972), the crown of pine is long (Valtanen 1994) and branches of pine and spruce appear in the low part of the stem (Salemaa et al. 1995, Salemaa and Lindgren 1998) in Northern Finland. The larger crown ratios are at least partly due to a lower density of forests in the Northern Finland (Hakkila 1971, Hakkila 1989, Salemaa and Lindgren 1998). Although the crowns are longer in Southern than in Northern Finland, trees are also taller in the South than in the North (Appendix 12), and therefore, the crown ratio of pine and spruce in the same diameter class is smaller in Southern Finland. For birch the results concerning the variability of the crown ratio were contradictory to pine and spruce. The proportion of downy birch is greater compared to silver birch in Northern than in Southern Finland (Valtanen 1994). Although the branchless proportion of the stem is greater in silver birch than in downy birch (Heiskanen 1957), in the NFI data used the crown ratio of birch in a certain diameter class was, however, generally larger on mineral soils in Southern than in Northern Finland.

Because of the slower growth rate, the amount of whorls can be supposed to be greater in Northern Finland. According to Salemaa et al. (1995) the branches of pine are usually thick, but according to Valtanen (1994) they are thin in Northern Finland. The branches of pine are short in Northern Finland (Salemaa et al. 1995, Valtanen 1994). The shortness of the branches is an adaptation of the trees to the northern conditions (Salemaa et al. 1995, Salemaa and Lindgren 1998), in which the amount of snow cover is large. According to Kuuluvainen (1988) narrow-crowned spruces possesses more needle and branch mass per unit of crown volume
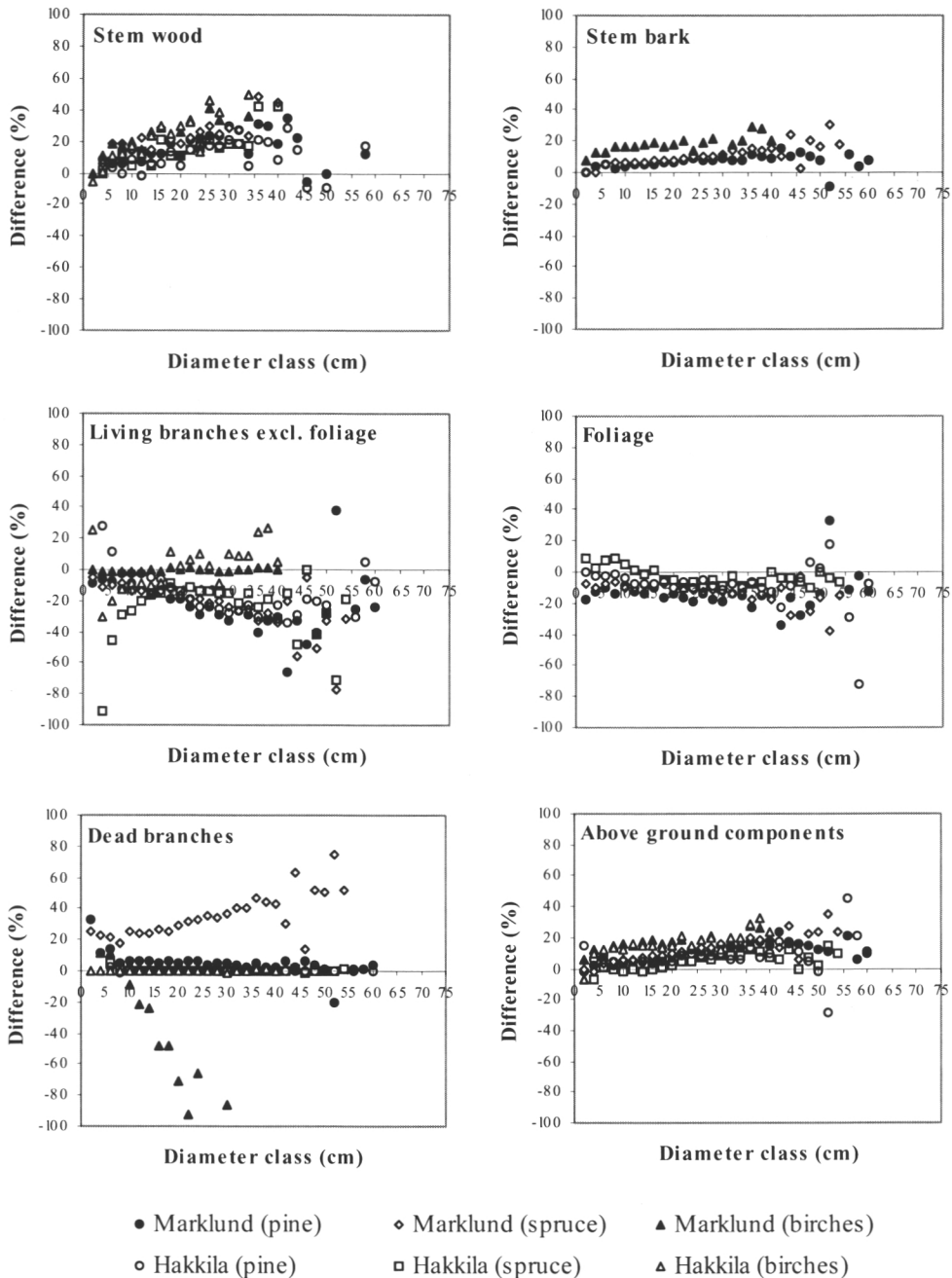
Figure 9. The relative differences in the biomass of single above-ground components of trees and in biomass of the sum of all above-ground components of trees estimated using Marklund's (1988) and Hakkila's (1979, 1991) models in Southern and in Northern Finland. The positive values mean that the biomass was higher in Southern Finland, and the negative values mean that the biomass was higher in Northern Finland. In the charts the differences were limited to ±100%.

than broad-crowned trees. However, pine had been observed to have more foliage per unit branch cross-sectional area, and also more branch cross-sectional area compared to stem cross-sectional area in the South than in the North (Nikinmaa et al. 1996). Based on these facts the biomass of branches can be assumed to be larger in the South than in the North. This is a contradictory conclusion to the outputs of Marklund's (1988) and Hakkila's (1991) models for pine and spruce.

Also for needles the estimates produced by the selected biomass models were bigger in Northern than in Southern Finland in most of the diameter classes (Figure 9). This result did not correspond to the previous studies. According to previous studies, the needles are short in Northern Finland (Salemaa et al. 1995), but the number of age classes of living needles is greater at high latitudes (Albrektson 1988, Salemaa et al. 1995, Reich et al. 1996, Petersson 1999). The amount of needles in one age class can be assumed to be, however, smaller in the North, because the annual shoots are shorter. Although e.g. Norway spruce carries its needles for a longer time in the North (Reich et al. 1996), the dry mass of needles of pine and spruce in the North is smaller than in the South (Hakkila 1972b).

Hakkila's (1991) biomass models for dead branches resulted in similar values for trees growing in different parts of Finland because they had only breast height diameter as an independent variable (Figure 9). When the biomass of dead branches of pine were estimated using Marklund's (1988) model, the differences between trees growing in Northern and in Southern Finland were small. Marklund's (1988) model produced lower estimates for biomass of dead branches of spruce in the North than in the South. Marklund's (1988) function for dead branches of birch gave larger estimates in Northern Finland than in Southern Finland. According to Hakkila et al. (1972), the length of stem appearing dead branches is larger in the same diameter class in Southern Finland than in Northern Finland. Spruces growing in Northern Finland have more dead branches within the living crown than those growing in Southern Finland (Hakkila 1971). Based on these studies, no conclusions about the biomass of dead branches in different parts of Finland could be made.

In most of the diameter classes the sums of the outputs of the models used in this study produce higher estimates for the biomass of the above-ground components in Southern than in Northern Finland (Figure 9). This result was supported by calculations made using Korhonen and Maltamo's (1990) model for the above-ground components of pine (Appendix 11).

Marklund's (1988) biomass model for stump and the model for roots, and Hakkila's (1972a) model for stump and roots had only breast height diameter as an independent variable, and thus, they produced no differences for trees growing in different parts of Finland. However, based on literature there are certain differences in the biomass of stump and roots in different locations. In Northern Finland pines have weak taproots or they have no taproots at all (Hakkila 1972a and 1976). According to Hakkila's (1972a) study, the differences in the biomass of stump-root system of pine were relatively small between Southern and Northern Finland. The stump-root system of spruce appeared to be larger in Northern Finland. There are no studies concerning the variation of the biomass of stump and roots of birch in different parts of Finland.

The proportions of stem wood of pine and spruce estimated by Marklund's (1988) models were greater in Southern than in Northern Finland, and the proportion of living branches and needles was greater in Northern than in Southern Finland. Also for birch, the variations of the proportions of stem wood and living branches were similar to those of pine and spruce. The differences in the percentages of stem bark and dead branches were not big for any tree species in different parts of the country. Because of the lack of representative studies, these results about the proportions of different above-ground components of a tree from the total above-ground biomass could not be compared with other studies.

3.2.2 Results on peatlands

By tree species

When the biomass of stem wood was estimated by Marklund's (1988) models, the ranking of tree species was rather similar on peatlands than on mineral soils (Figures 4 and 10). The main difference was, that on peatlands Marklund's (1988) model generally gave larger biomass values for spruce stem wood than for birch stem wood already in the diameter classes >30 cm. On mineral soils, the biomass estimates were greater for spruces than birches in diameter classes ≥39 cm. Also the stem wood estimates of Hakkila's (1979) biomass models for trees growing on peatlands correspond well to those for trees growing on mineral soils, when the ranking on tree species was considered. However, the biomass estimates of pines were larger than that of spruce in diameter classes >35 cm; the corresponding classes on mineral soil were >30 cm. According to NFI data the rankings of tree height, stem wood volume and stem wood density of different tree species were rather similar on peatlands and on mineral soils (Appendices 9 and 13). The small differences in the ranking of stem wood biomass could, however, be explained in small differences in the ranking of tree heights on peatlands and on mineral soils.

Like on mineral soils, the outputs of Marklund's (1988) and Hakkila's (1991) models for living branches were the smallest for pine. The ranking of the estimates of Marklund's (1988) models concerning spruce and birch corresponded to the ranking on mineral soils. Also the ranking of outputs of Hakkila's (1991) models concerning spruce and birch corresponded to the ranking on mineral soils. On peatlands the rankings of the biomass of needles and dead branches estimated by Marklund's (1988) and Hakkila's (1979, 1991) models, according to tree species, corresponded well to the rankings on mineral soils. In the NFI data the crown lengths of trees growing peatlands did not differ much from those of trees growing on mineral soils in the same diameter classes (Appendices 9 and 13).

When the ranking of the tree species were considered, the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models for the different above-ground components generally corresponded rather well with the outputs of the peatland models in the diameter range of the modeling data of the peatland models (Figures 10 and 11). Marklund (1988) and Hakkila (1979, 1991) did not have models for the

Figure 10. The biomass of single above-ground components of trees and the biomass of the sum of all above-ground components of trees by tree species estimated using Marklund's (1988) and Hakkila's (1979, 1991) models in different diameter classes on peatlands.
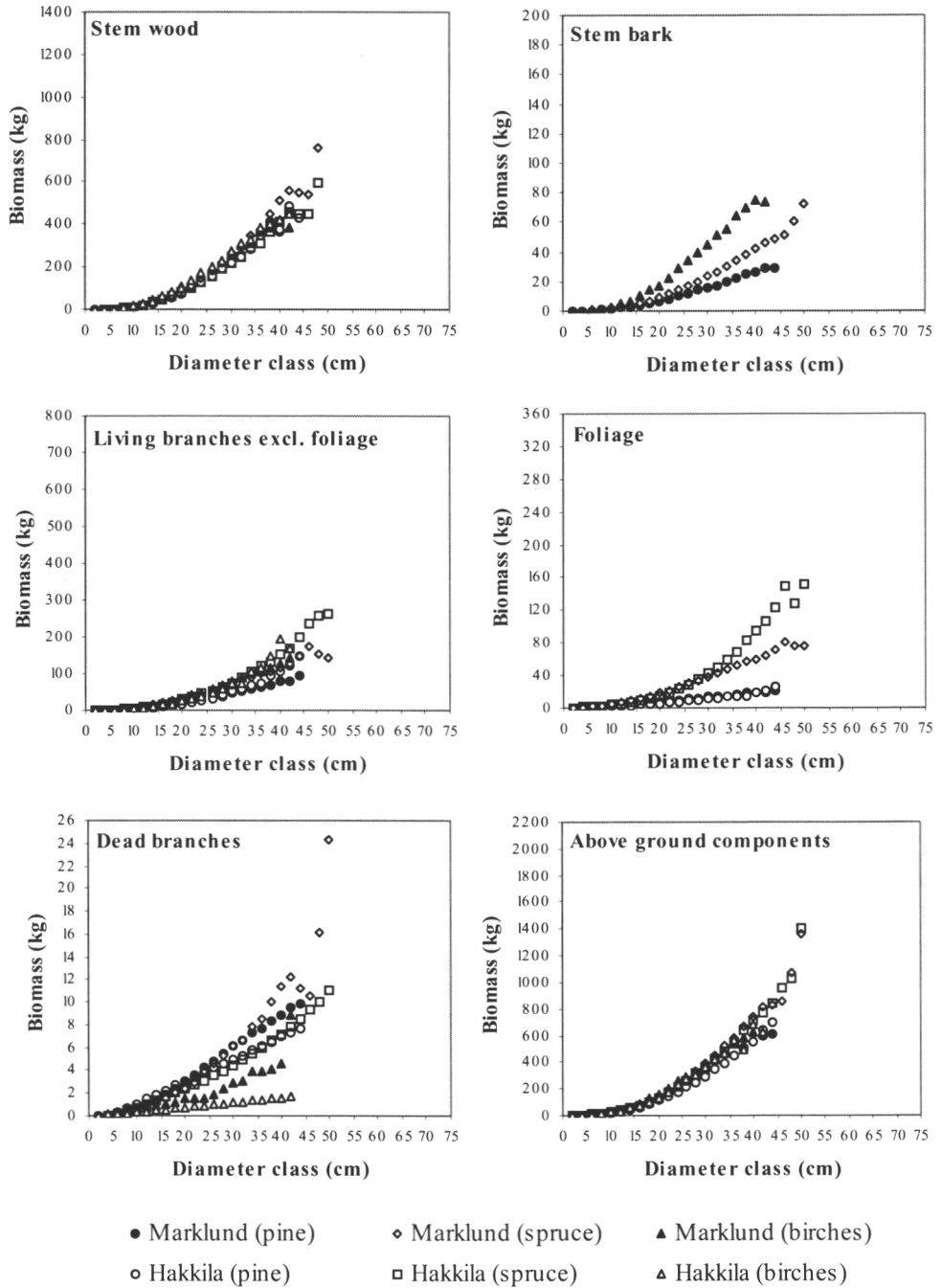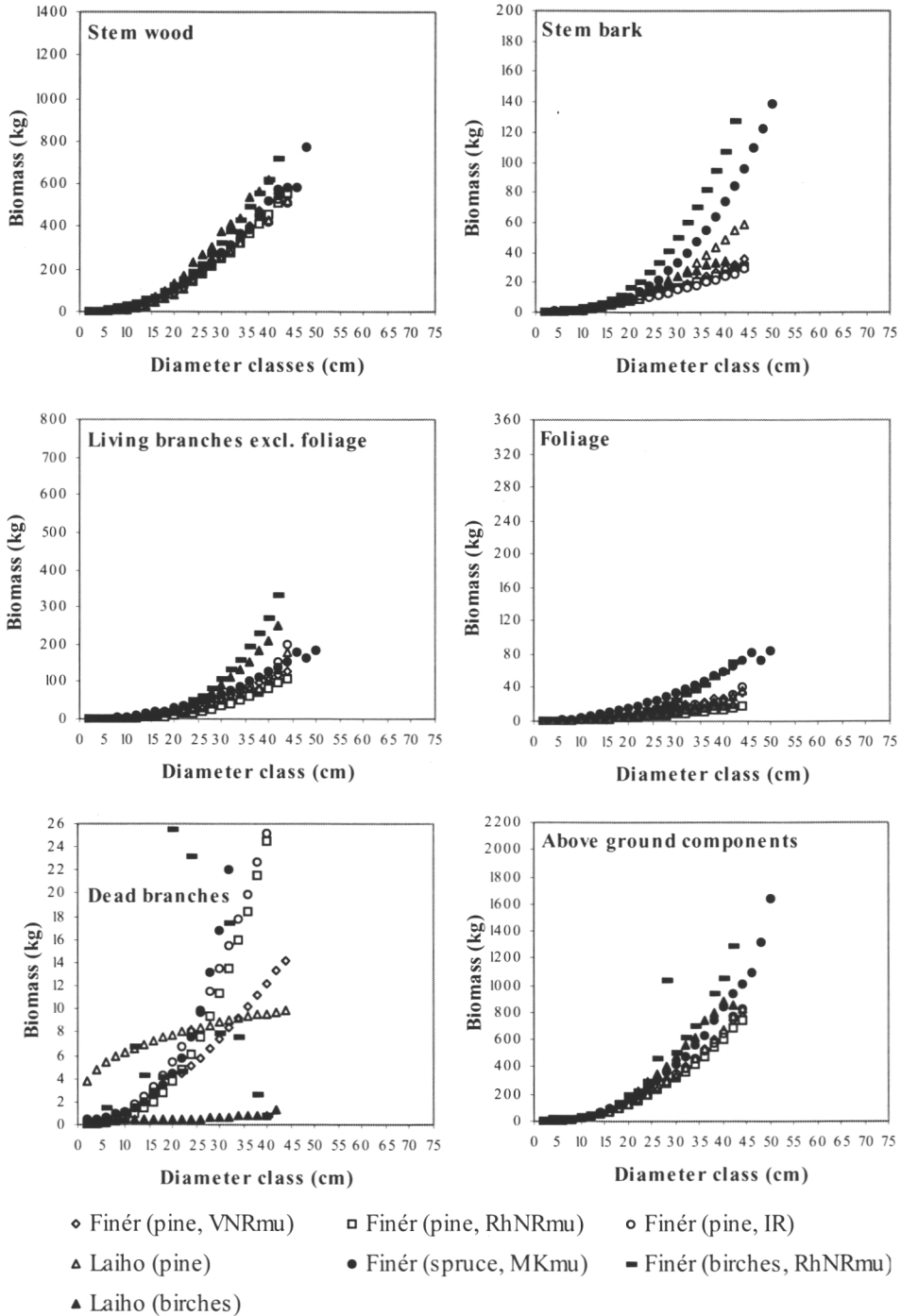
Figure 11. The biomass of single above-ground components of trees and the biomass of the sum of all above-ground components of trees by tree species estimated using Finér's (1989, 1991) and Laiho's (1997) models in different diameter classes on peatlands.

biomass of leaves of birch. According to estimates produced by Finér's (1989) and Laiho's (1997) models, the biomass of leaves of birch were about the same or lower than the biomass of pine needles. The ranking of the outputs of Marklund's (1988) and Hakkila's (1972a) models for biomass of stump and roots between pine and spruce was coincident with the outputs of the studied peatland models (Figures 5 and 12). Marklund (1988) and Hakkila (1972a) did not have models for stump and roots of birch. Issakainen's (1988) models produced similar estimates for the biomass of stump and roots for pine and birch in the diameter range of the data used for the formulation of the models (Figure 12).
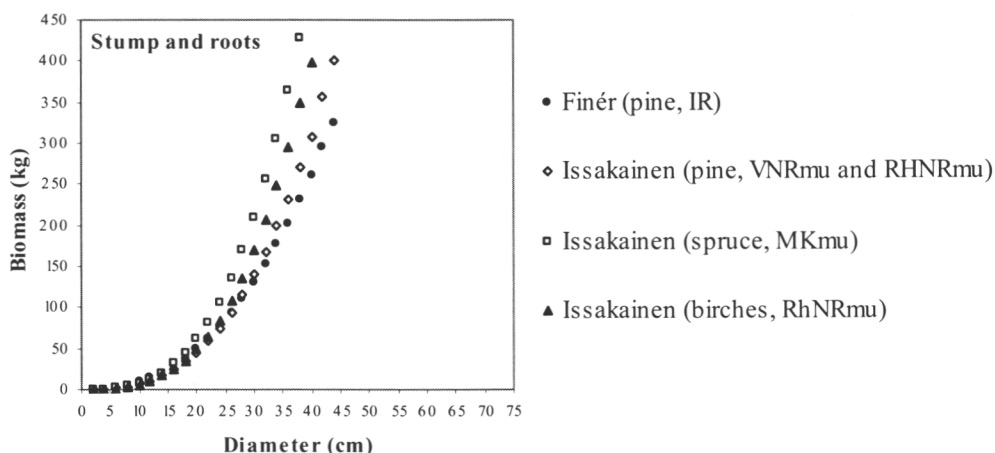
Figure 12. The biomass of stump and roots of pines, spruces and birches estimated using Issakainen's (1988) and Finér's (1991) models in different diameter classes on peatlands.

By size of tree

The comparisons between the outputs (Figures 6 and 13) and the standard deviations of the outputs (Figures 7 and 14) of Marklund's (1988) and those of Hakkila's (1979, 1991) models in different diameter classes on peatlands corresponded rather well with those made on mineral soils. One exception was the biomass of pine needles. On mineral soils the outputs of the models for biomass of pine needles differed less than 20% for a very wide diameter range, but on peatlands this was only the case in the larger diameter classes.

The comparison between the outputs of the mineral soil models and those of peatland models showed that the magnitudes of the biomass of components of trees were about the same in the range of the modeling data of the peatland models (Figures 10 and 11). Outside the range of the data of the peatland models most of the peatland models produced unreasonable estimates. When different models from Finér (1989, 1991) were studied, there were large differences in the biomass they produced. It was, however, possible to identify a set of Finér's (1989, 1991) mod-

Figure 13. The relative differences in the biomass of single above-ground components of trees and in the biomass of the sum of all above-ground components of trees estimated using Marklund's (1988) and Hakkila's (1979, 1991) models on peatlands. The positive values mean that Marklund's (1988) models produced higher values than Hakkila's (1979, 1991) models, and the negative values mean that Marklund's (1988) models produced lower values than Hakkila's (1979, 1991) models. In the charts the differences were limited to ±100%.

○ pine   ◇ spruce   ▲ birches
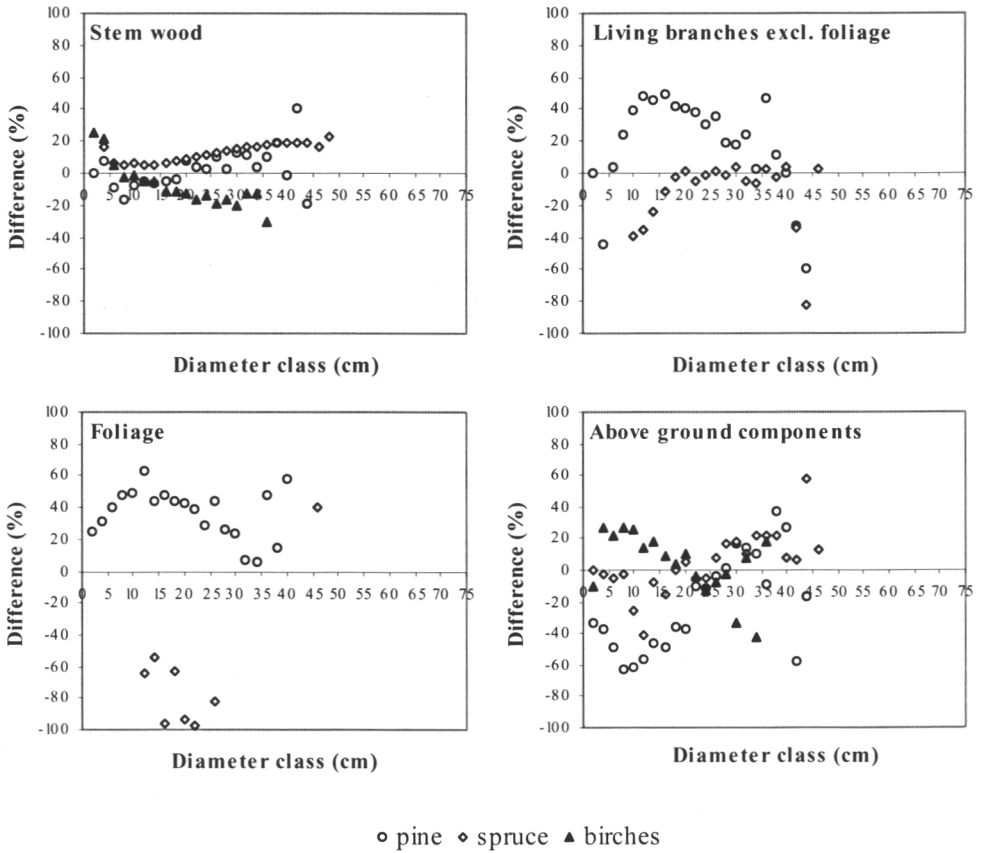
Figure 14. The relative differences between the standard deviations of the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models in different diameter classes on peatlands. The positive values mean that the standard deviations of the outputs of Marklund's (1988) models were higher than those of Hakkila's (1979, 1991) models, and the negative values mean that the standard deviations of the outputs of Marklund's (1988) models were lower than those of Hakkila's (1979, 1991) models. In the charts the differences were limited to ±100%.

els for stem wood, living branches and needles of pine and spruce, which corresponded rather well with either Marklund's (1988) or Hakkila's (1979, 1991) models. For birch the variation between the outputs of mineral soil models and peatland models was larger. For pine and birch the outputs of Laiho's (1997) biomass models for stem wood, living branches and needles corresponded moderately well to those of Marklund's (1988) or Hakkila's (1979, 1991) models in the range, and even outside this range, of Laiho's (1997) modeling data. The differences between the outputs of peatland models and those of Marklund's (1988) and Hakkila's (1979, 1991) models were the largest when the biomass of dead branches was studied. Generally, there was no divergent trend in the biomass estimates of

components of trees growing on the peatlands when compared to trees growing on the mineral soils.

By location

In all studied tree species Marklund's (1988) and Hakkila's (1979) functions produced higher estimates for the biomass of stem wood for peatlands in Southern than in Northern Finland. Marklund's (1988) model produced higher estimates for bark biomass on peatlands in Southern than in Northern Finland (Figure 15). Marklund's (1988) models for pine and spruce, and Hakkila's (1991) models for all species generally resulted in larger biomass of living branches and biomass of needles in Northern than in the Southern Finland. Thus, on peatlands the differences in outputs of Hakkila's (1991) model for living branches of birch in Southern and in Northern Finland were in contrast to those on mineral soils. The reason for these differences was that, according to NFI data used, on mineral soils the crown ratios (which was used as an independent variable in Hakkila's (1991) model for living branches of birch) were generally larger in a certain diameter class in trees growing in Southern than in Northern Finland, but on peatlands the crown ratios were larger in Northern Finland. Marklund's (1988) model for biomass of living branches of birch and Hakkila's (1991) models for dead branches of all studied tree species had only diameter at breast height as an independent variable, and thus, they produced similar estimates irrespective of the location. Marklund's (1988) models for the biomass of dead branches of pine and spruce resulted in larger estimates in Southern than in Northern Finland. For the biomass of dead branches of the thinnest birches, Marklund's (1988) model produced larger values in Southern than in Northern Finland. For the larger diameter trees (>8 cm) the model produced larger values for Northern Finland. The biomass estimates of the above-ground components of trees as a whole were commonly larger in Southern than in Northern Finland. Generally, these results agreed well with the results for trees growing on mineral soils. Also the estimates about the differences in tree height, crown length, stem volume and stem wood density between Southern and Northern Finland corresponded with those for trees growing on mineral soils (Appendix 15).

For the peatland models that also have other independent variables in addition to breast height diameter, the stem wood biomass estimates were larger in Southern than in Northern Finland (Figure 16). When the biomass of stem bark of pine and birch were considered, Laiho's (1997) models gave results, which were in accordance to the results of the mineral soil models. Finér's (1991) function for the biomass of stem bark of pine resulted in higher values in Northern than in Southern Finland; this was the opposite result to the results of Laiho's (1997) model and the mineral soils models.

According to the mineral soil models, the biomass of living branches and needles were larger in northern than in southern pines and spruces; this corresponded well with the peatland models (Figures 15 and 16). When the biomass of dead branches of pine was estimated using Marklund's (1988) model, the biomass estimates were larger in the Southern Finland. For the biomass of dead branches of pine, Finér's (1989, 1991) and Laiho's (1997) models did not produce large differ-
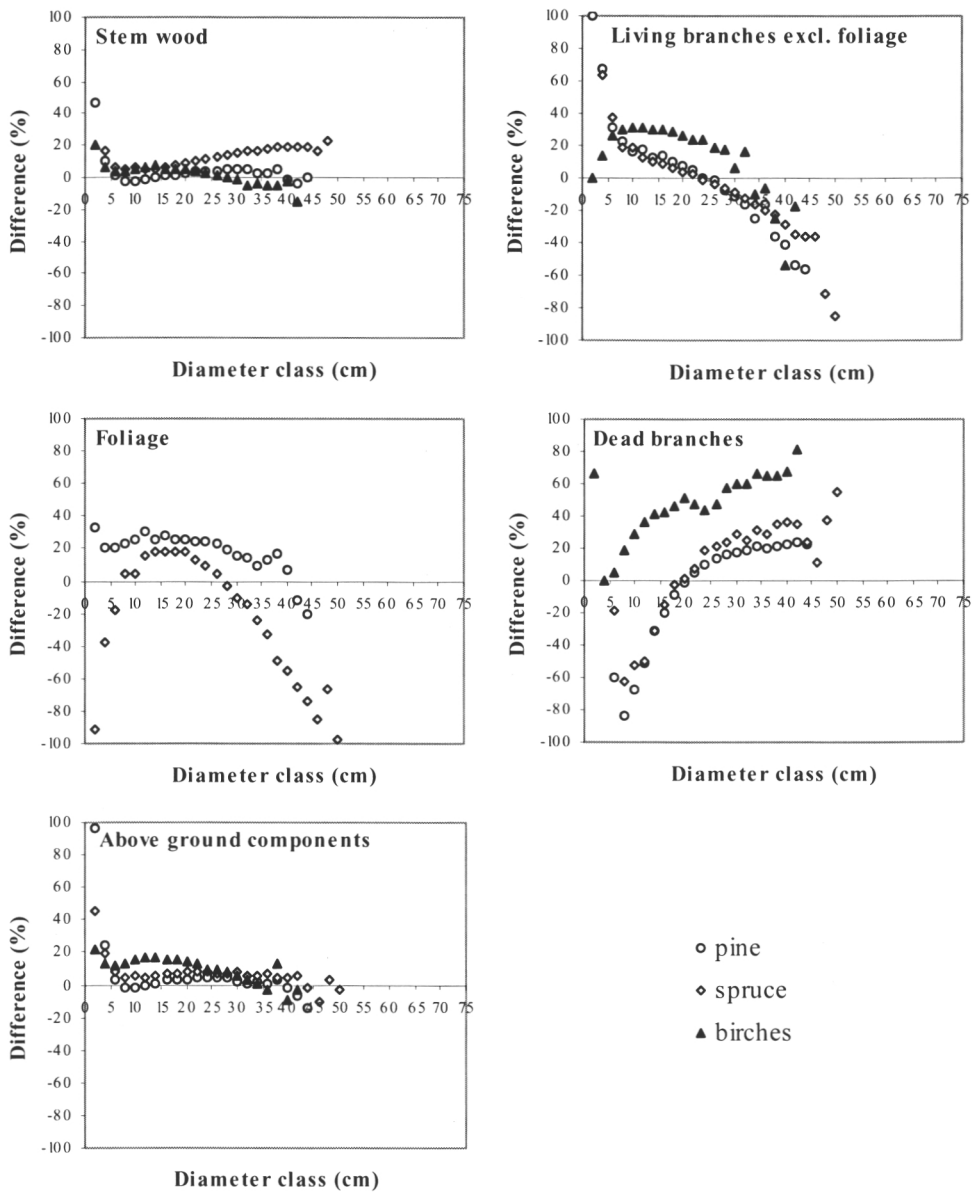
Figure 15. The relative differences in the biomass of single above-ground components of trees and in the biomass of the sum of all above-ground components of trees estimated using Marklund's (1988) and Hakkila's (1979, 1991) models on peatlands in Southern and in Northern Finland. The positive values mean that the biomass is higher in Southern than in Northern Finland, and the negative values mean that the biomass is lower in Southern than in Northern Finland. In the charts the differences were limited to ±100%.

Figure 16. The relative differences in the biomass of single above-ground components of trees and in the biomass of the sum of all above-ground components of trees estimated using Finér's (1989, 1991) and Laiho's (1997) models having in addition to breast height diameter also other independent variables on peatlands in Southern and Northern Finland. The positive values mean that the biomass was higher in Southern than in Northern Finland, and the negative values mean that the biomass was lower in Southern than in Northern Finland. In the charts the differences were limited to ±100%.

ences in different parts of Finland. Finér's (1989, 1991) models only had breast height diameter as an independent variable. Laiho's (1997) model had relative tree height in addition to breast height diameter as an independent variable, but in this study, relative tree height had no effect on the biomass estimates (see the chapter 3.1.5). On peatlands, Marklund's (1988) function for biomass of dead branches of spruce produced larger values in Southern than in Northern Finland. For the biomass of dead branches of birch, Laiho's (1997) function gave larger values in Northern than in Southern Finland; this was a similar result to the results of Marklund's (1988) model. Finér's (1989) model for biomass of dead branches of birch produced larger estimates in Southern than in Northern Finland. The outputs of Finér's (1989) models for the biomass of dead branches of birch were, however, not reasonable in many diameter classes. Generally, the estimates of both mineral soil models and peatlands models for the total above-ground biomass of a tree were higher in the South than in the North.

Peatlands vs. mineral soils

Both Marklund's (1988) and Hakkila's (1979) models produced generally larger estimates for stem wood of all considered tree species on mineral soils than on peatlands (Figure 17). For the stem bark of pine and birch, Marklund's (1988) models produced slightly lower estimates on peatlands than on mineral soils. In spruce, Marklund's (1988) function gave rather similar values for the biomass of bark on both peatlands and mineral soils. For the NFI data, the mean heights and mean volumes of trees were larger in the same diameter classes on mineral soils than on peatlands. The stem wood densities estimated as a relation between Marklund's (1988) biomass models and Laasasenaho's (1982) volume functions and Hakkila's (1979) density models did not differ on mineral soils and on peatlands (Appendix 14).

The biomass of living branches of pine and spruce were slightly larger on peatlands when they were calculated using either of the mineral soil models (Figure 17). Excluding the thinnest and the thickest trees, Hakkila's (1991) function for living branches of birch did not give large differences between peatlands and mineral soils. Marklund's (1988) model for pine needles gave larger estimates on peatlands than on mineral soils. Hakkila's (1991) function produced the opposite results. However, both of the models produced small differences between peatlands and mineral soils. When biomass of needles of spruce estimated using considered models were studied, the differences on mineral soils and peatlands were generally quite low. In the used NFI data, the crowns were longer on mineral soils than on peatlands (Appendix 14). Otherwise these results were not able to be evaluated because of the lack of representative studies. Marklund's (1988) models for dead branches produced higher values for pines and spruces growing on mineral soils than on peatlands. For dead branches of birch, Marklund's (1988) model resulted in higher values on peatlands than on mineral soils. Hakkila's (1991) models did not produce differences in different sites, because they had only breast height diameter as an independent variable. The differences in the biomass of single components of a tree were usually low between the trees in the same diameter classes on mineral
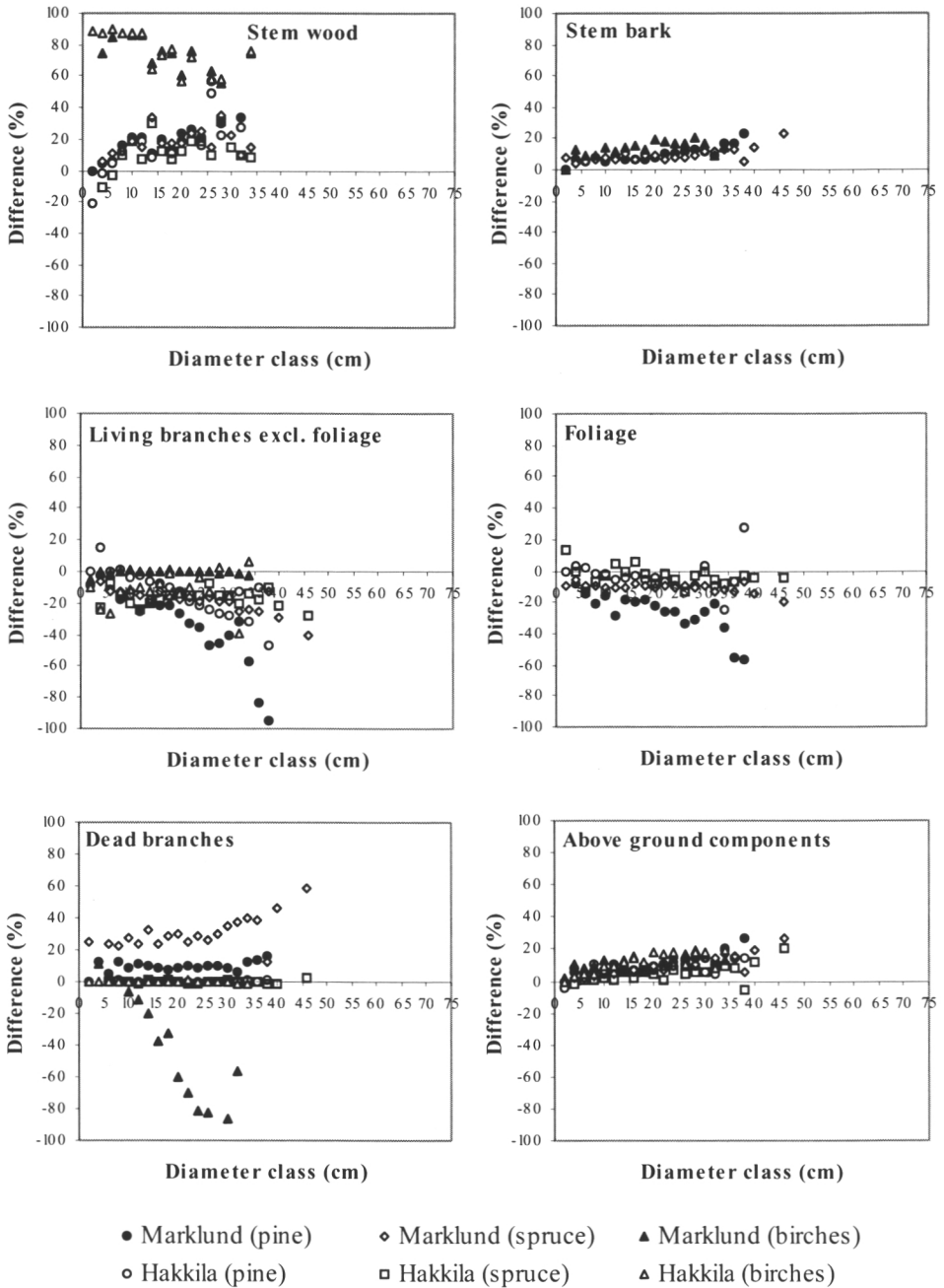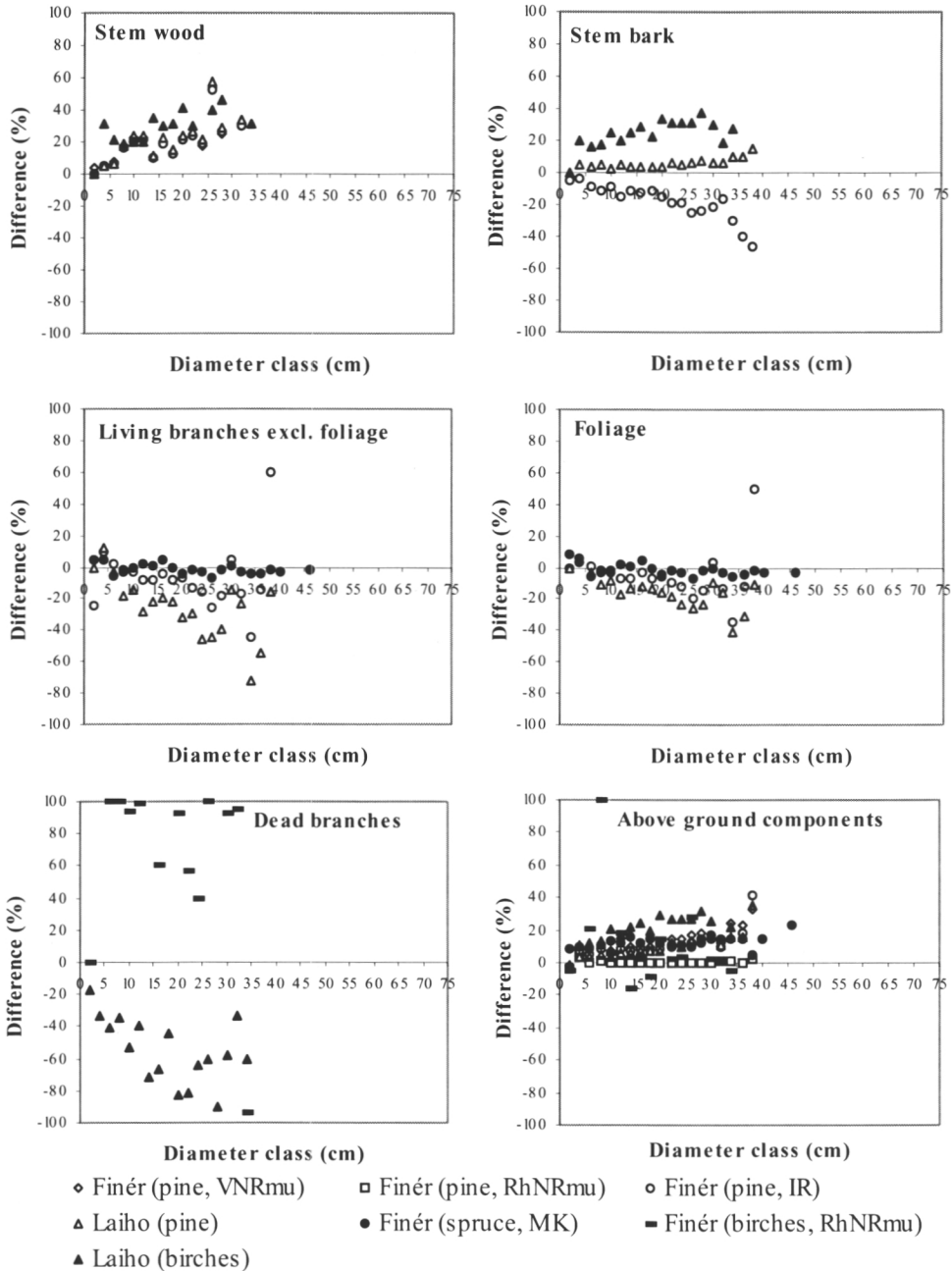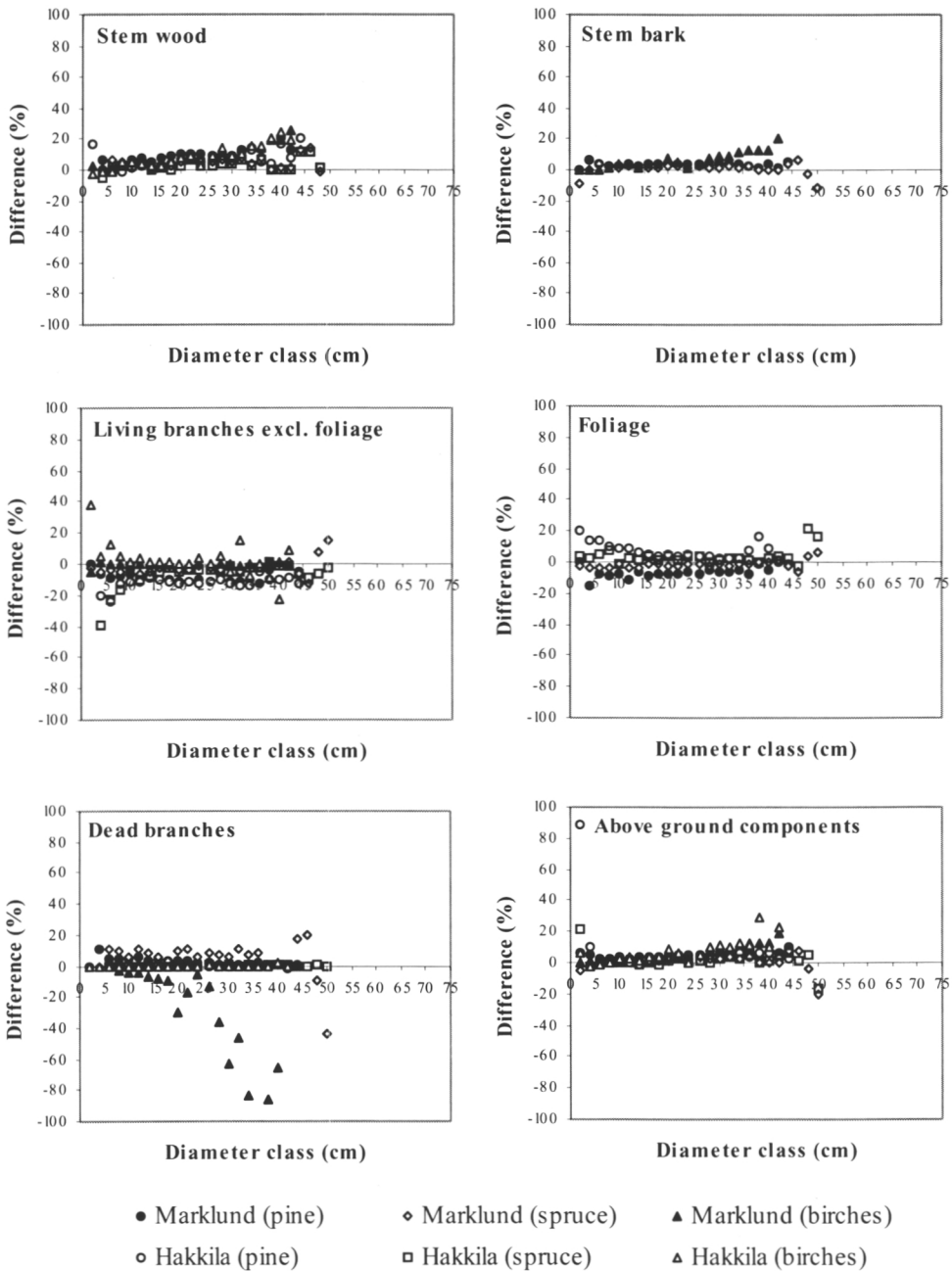
Figure 17. The relative differences in the biomass of single above-ground compo-
nents of trees and in the biomass of the sum of all above-ground components of
trees estimated using Marklund's (1988) and Hakkila's (1979, 1991) models on
mineral soils and on peatlands. The positive values mean that the biomass esti-
mates were higher on mineral soils than on peatlands, and the negative values mean
that the biomass estimates were lower on mineral soils than on peatlands. In the
charts the differences were limited to ±100%.

soils and on peatlands, and therefore, also the differences in the biomass of the above-ground components as a whole were small between these sites. In most of the diameter classes, the biomass of the above-ground components was a little larger on mineral soils than on peatlands.

3.2.3 Applicability of the biomass models for trees growing on different sites and in different locations

On both mineral soils and on peatlands Marklund's (1988) and Hakkila's (1979, 1991) models produced similar outputs for many tree components. On peatlands, there were no consistent differences between the outputs of Finér's (1989, 1991) and Laiho's (1997) models when compared to those of Marklund's (1988) and Hakkila's (1979, 1991) models. Thus, based on this result, Marklund's (1988) and Hakkila's (1979, 1991) models can be applied for the estimation of the biomass of trees growing on peatlands. However, Finér's (1989, 1991) and Laiho's (1997) models cannot be considered representative for more specific evaluation of the variability of the biomass along e.g. location.

When only the ranking of the biomass of different tree species was considered, Marklund's (1988) and Hakkila's (1979, 1991) models were the most applicable for the estimation of different components of pines and birches both on mineral soils and on peatlands (Table 11). The models also produced reasonable results for biomass of living branches, needles and above-ground components of spruces in relation to pines both on mineral soils and on peatlands. Thus, these models seem applicable in this respect. When the ranking of different tree species was studied, the most uncertainty was included for the estimation of stem wood biomass of pine and spruce on mineral soils, and living branches of spruce and birch on both mineral soils and on peatlands.

According to the comparisons between the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models in different diameter classes, the models were the most applicable for the estimation of biomass of stem wood and above-ground components of a tree (Table 12). For pine and spruce the models for living branches can also be applied for the estimation of the biomass of middle-sized trees. On mineral soils the biomass of foliage of pine and spruce, and on peatlands the biomass of foliage of spruce can be estimated by the studied models. Based on the comparisons of the models much uncertainty was included for the estimation of foliage of pine on peatlands, and for the estimation of dead branches of all tree species both on mineral soils and on peatlands.

Generally, Marklund's (1988) models can be used for the estimation of the biomass of different components of trees having different sizes because they do not produce negative values or unrealistically high or low estimates. When Hakkila's (1972a, 1979, 1991) models are applied, some limitations have to be taken into account. The subtraction between Hakkila's (1991) models for living branches and needles of pine and spruce produced negative values, and thus, they cannot be used for the smallest trees. Hakkila's (1991) models for dead branches of all tree species and Hakkila's (1972a) models for stump and roots of pine and birch cannot be ap-

plied for the smallest trees for the same reason. The unrealistically high values for the trees in the larger diameter classes was given by Hakkila's (1991) models for living branches of all tree species, and the model for spruce needles. Therefore, these models are not applicable for the largest diameter trees.

Table 11. Comparisons of Marklund's (1988) and Hakkila's (1972a, 1979, 1991) biomass models by ranking of tree species on mineral soils and on peatlands. Other studies refer to the studies mentioned in chapter 3.2.1 (section '*By tree species*') concerning mineral soils. On peatlands separate comparisons with the other studies were not made because of the lack of studies. Explanations of the colors: blue = outputs correspond in >75% of diameter classes (outputs correspond with other studies); yellow = outputs correspond in 51-75% of diameter classes (outputs partly correspond with other studies); red = outputs correspond in <51% of diameter classes (outputs do not correspond with other studies); light blue = outputs of Marklund's (1988) models correspond with other studies; orange = outputs of Marklund's (1988) models do not correspond with other studies; white = outputs cannot be compared because of lack of models (outputs cannot be compared because of lack of other studies).

| | MARKLUND (1988) vs. HAKKILA (1972a, 1979, 1991) | | | | | | STUDIED MODELS vs. OTHER STUDIES | | |
| | Mineral soils | | | Peatlands | | | Mineral soils | | |
	Pine vs. Spruce	Pine vs. Birch	Spruce vs. Birch	Pine vs. Spruce	Pine vs. Birch	Spruce vs. Birch	Pine vs. Spruce	Pine vs. Birch	Spruce vs. Birch
Stem wood	red	blue	yellow	blue	blue	yellow		light blue	light blue
Stem bark							light blue	light blue	light blue
Living br.	blue	blue	red	red	blue	red			
Foliage	blue		blue		blue		blue		
Dead branches	yellow	blue	blue	yellow	blue	blue	yellow	blue	blue
Stump and roots	blue			yellow			yellow		
Above ground comp.	blue	blue	yellow	blue	yellow	yellow	blue	blue	yellow

Table 12. Diameter classes of trees growing on mineral soils and on peatlands, in which Marklund's (1988) models differed less than 20% from Hakkila's (1979, 1991) models.

| | MINERAL SOILS | | | PEATLANDS | | |
	Pine	Spruce	Birch	Pine	Spruce	Birch
Stem wood	9-55	7-56 (62)	6-53	3-40 (44)	3-44	1-34 (42)
Stem bark						
Living branches excl. foliage	10-33	10-36	25-38	9-33	8-36	25-36
Foliage	2-46	7-31		28-43	6-33	
Dead branches	16-32	14-22	3-8	17-33	16-25	3-8
Above ground components	5-52	4-52 (60)	2-47	5-44	4-53	3-42

The results concerning proportion of the components estimated using Marklund's (1988) models could not be properly compared with the other studies, because of the lack of studies. However, the outputs of Marklund's (1988) models corresponded rather well with single studies (see chapter 3.2.1, section '*By size of tree*'), when the trees of different sizes were considered.

The reactions of Marklund's (1988) and Hakkila's (1979) models for the biomass of stem wood on the changes in site (fertile or infertile) and in location (Southern or Northern Finland) are in accordance with conclusions made in other studies and the NFI data (Tables 13 and 14, see also chapter 3.2.1, sections '*By site fertility*' and '*By location*').

Table 13. Comparisons of the outputs of Marklund's (1988) and Hakkila's (1972a, 1979, 1991) biomass models by tree species on different sites. Other studies refer to the literature mentioned and the analysis made using the NFI data in chapter 3.2.1 (section '*By site fertility*') concerning the reaction to site fertility. See the explanations of the colors from Table 11.

	MINERAL SOILS						MINERAL SOILS VS. PEATLANDS		
	Reaction to site fertility						Course of variation between mineral soils and peatlands		
	Marklund vs. Hakkila			Studied models vs. Other studies			Marklund vs. Hakkila		
	Pine	Spruce	Birch	Pine	Spruce	Birch	Pine	Spruce	Birch
Stem wood	blue	blue	blue	blue	blue	blue	blue	blue	blue
Stem bark	white	white	white	light blue	light blue	light blue	white	white	white
Living br.	blue	blue	red	red	red	red	blue	blue	red
Foliage	blue	blue	white	red	red	white	blue	blue	white
Dead br.	red	red	red	white	white	white	red	red	red
Stump	white	white	white	white	white	white	white	white	white
Roots	white	white	white	orange	orange	white	white	white	white
Stump and roots	blue	blue	white	white	white	white	blue	blue	white
Above gr. comp.	blue	blue	blue	blue	white	white	blue	yellow	blue

Also the estimates of stem bark produced by Marklund's (1988) models are reasonable for trees growing on different sites and locations. Based on comparisons between the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models, the biomass of above-ground components of pines and birches can also be estimated on different sites and locations using these models. More uncertainty is included in the estimates of the biomass of above-ground components of spruces. The examined Marklund's (1988) and Hakkila's (1991) functions for living branches and needles of pine and spruce produce contradictory results on different site fertilities and in different parts of Finland when compared to conclusions from other studies and the NFI data. Hakkila's (1991) model for living branches of birch produced in many diameter classes higher estimates in Southern than in Northern Finland; this may correspond to the real situation, but no conclusions could be made based on reference material about the variability of the biomass of living branches of birch.

The comparison of the differences in the biomass of needles on peatlands and on mineral soils estimated by Marklund's (1988) and Hakkila's (1991) models gave contradictory results. Marklund's (1988) models for the biomass of living branches of birch and for the biomass of stump and that for roots of pine and spruce, and Hakkila's (1991) models for the biomass of dead branches of all tree species and that of stump and roots of pine and spruce have only breast height diameter as an independent variable, and thus, they cannot take into account the variability of tree biomass according to site and location. In summary, much uncertainty is included in the estimation of the biomass of foliage, living branches, dead branches, stump and roots.

Table 14. Comparisons of the outputs of Marklund's (1988) and Hakkila's (1972a, 1979, 1991) biomass models by tree species in different locations. Other studies refer to the literature mentioned and the analysis made using the NFI data in chapter 3.2.1 (section '*By location*') concerning the reaction to location (in Northern or Southern Finland) on mineral soils. See the explanation of the colors from Table 11.

| | MINERAL SOILS | | | | | | PEATLANDS | | |
| | Marklund vs. Hakkila | | | Studied models vs. Other studies | | | Marklund vs. Hakkila | | |
	Pine	Spruce	Birch	Pine	Spruce	Birch	Pine	Spruce	Birch
Stem wood	blue	blue	blue	blue	blue	blue	blue	blue	blue
Stem bark	white	white	white	light blue	light blue	light blue	white	white	white
Living br.	blue	blue	red	red	red	white	blue	blue	red
Foliage	blue	yellow	white	red	red	white	blue	yellow	white
Dead br.	red	red	red	white	white	white	red	red	red
Stump	white	white	white	white	white	white	white	white	white
Roots	white	white	white	orange	white	white	white	white	white
Stump and roots	blue	blue	white	red	red	white	blue	blue	white
Above gr. comp.	blue	yellow	blue	blue	white	white	blue	blue	blue

3.3 Applicability of the biomass models for the forestry modeling and analyses: Case study

3.3.1 Incorporation of selected biomass models into the MELA system

In the case study, Marklund's (1988) and Hakkila's (1979, 1991) biomass models for the different above-ground components of a tree represented in Tables 8 and 9 were incorporated into the MELA forest planning system (Siitonen et al. 1996, Hynynen et al. 2002, Redsven et al. 2004). The objective was to determine if the choice of the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models as a constraint in optimizations affects the selection of optimal management schedules in the MELA system. In addition, the differences between the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models were studied at the forest area

level. Furthermore, the influences of different biomass constraints on the net carbon sequestration of the trees were analyzed.

Only the biomass models for the different above-ground components of a tree were incorporated into the MELA because Marklund's (1988) and Hakkila's (1972a) models for stump and roots take into account different proportions of these components (see chapter 3.1.3). Due to the lack of models some adjustments had to be made when the biomass models were incorporated into the MELA. Because neither Marklund (1988) nor Hakkila (1991) have models for the biomass of foliage for birch, the models for needles of pine were used instead. Based on comparisons with the previous studies (Mälkönen 1977, Kubin 1982, Mälkönen and Saarsalmi 1982, Finér 1989, Kauppi et al. 1995, Laiho 1997), the biomass of leaves of birch can be assumed to correspond rather well with the biomass of pine needles (Appendix 16). Other deciduous trees in addition to birch were treated as birch, and other conifers in addition to pine and spruce, were treated as pine in the biomass estimations. Hakkila's (1979) model for the biomass of stem over bark was used instead of separate models for stem wood and for stem bark, because the calculation of the biomass of stem bark was unreasonable as a difference between stem over bark and stem wood (see section 'By size of tree' in chapter 3.2.1).

Based on the analyses about the range of applicability of the models made in chapter 3.2.1 (section 'By size of tree') some limitations were implemented for Hakkila's (1979, 1991) biomass models. If a biomass model of a component gave a value <0 kg, the biomass of a component was supposed to be 0 kg. The biomass of living branches of birches having height ≤2 m was supposed to be 0 kg. Hakkila's (1991) models for the living branches of all considered tree species and for needles of spruce produced unreasonably high biomass estimates for the thickest trees, but no limits were set for the biomass.

3.3.2 Data for the MELA analyses

The data used in the MELA simulations were chosen to closely represent the forest structure in Southern Finland (see Finnish Statistical Yearbook of Forestry 2003). The data were comprised of 185 stands from the research forests of the Finnish Forest Research Institute in Suonenjoki (62°39'N, 27°03'E) in the area of the province Northern Savo in central Finland. The total area was 205.5 ha, of which 79% was mineral soils and 21% peatlands. The proportion of area of peatlands was a little smaller in the data from Suonenjoki than in Southern Finland. According to the dominant tree species, pine stands accounted for 50% of the area, spruce stands 38%, and birch stands 12% of the total area. Pine, spruce and birch accounted for 39%, 39% and 22% of the total volume, respectively. The percentage of the area of spruce-dominated stands was a little greater in the data than in Southern Finland. The proportion of volume of different tree species was almost the same in the study data as for Southern Finland (Figure 18).

In the study data, on mineral soils all the spruce- and birch-dominated stands were located on fertile sites. Most of pine-dominated stands were on fertile mineral soils (45% of area, 50% of volume). Over half of the area of peatlands was domi-
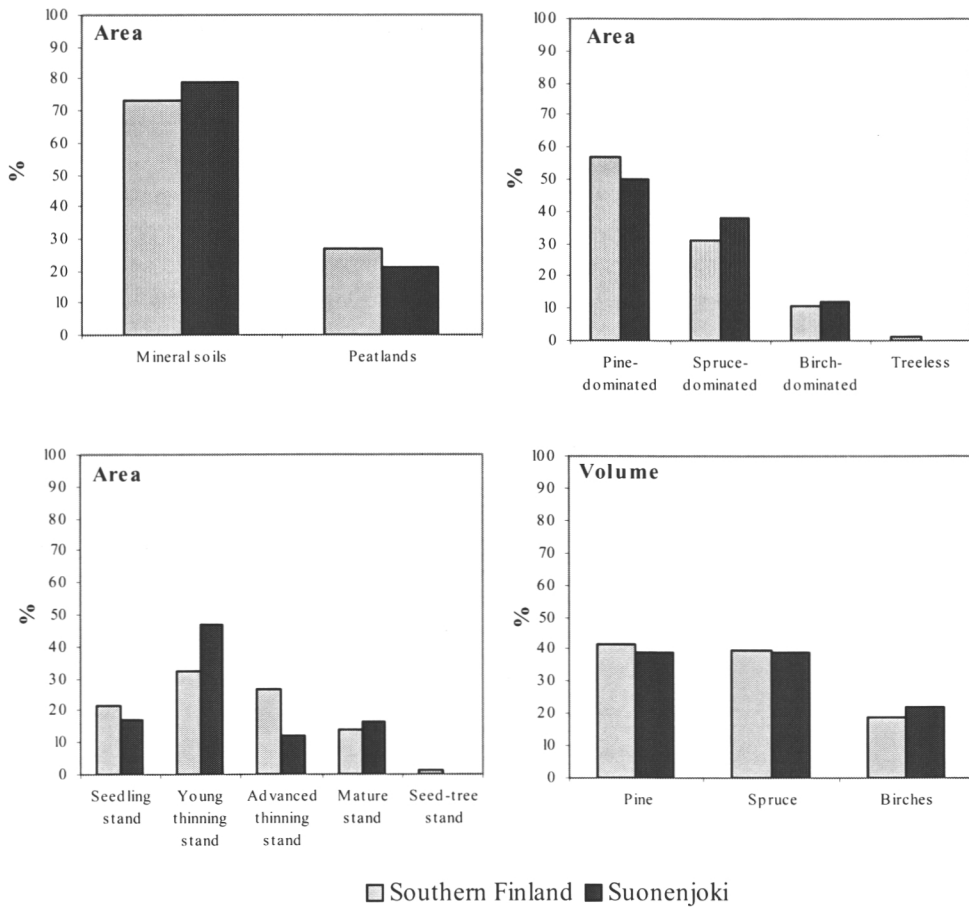
□ Southern Finland ■ Suonenjoki

Figure 18. The structure of the data used in MELA simulations compared to that estimated in Southern Finland (Finnish Statistical Yearbook of Forestry 2003).

nated by pine, and the proportions of the area of both spruce- and birch-dominated stands were a little over 20%. On peatlands, the proportions of pine-, spruce- and birch-dominated stands were about one-third of the total volume.

The proportion of the area of young thinning stands was greater, and the area of advanced thinning stands was smaller, for the study data than in Southern Finland (Figure 18). In the study data, especially the area of pine-dominated young thinning stands was large. The proportions of advanced thinning stands of spruce and that of mature stands of spruce and pine from the total volume were high (Figure 19).

There were no mature stands of birch on the mineral soils, and only one on peatlands. The area of seedling stands of birch was also small. In the study data, the division of stands to the different development classes was based on the diameter limits of recommendations of Forestry Center Tapio in 2001 (Metsätalouden kehittämiskeskus Tapio 2001). However, the young seedling stands and advanced seed-

ling stands were treated together. In order to decrease the amount of different classes, the treeless regeneration area was incorporated into seedling stands. Based on diameter, stands in seed-tree position and shelterwood stands were classified as mature stands. The classification of hold-over seedling stands was made according to the breast height diameter of hold-overs. The other determinations for development classes used in the recommendations in addition to breast height diameter (mean age, dominant height) were not taken into account in the classification.
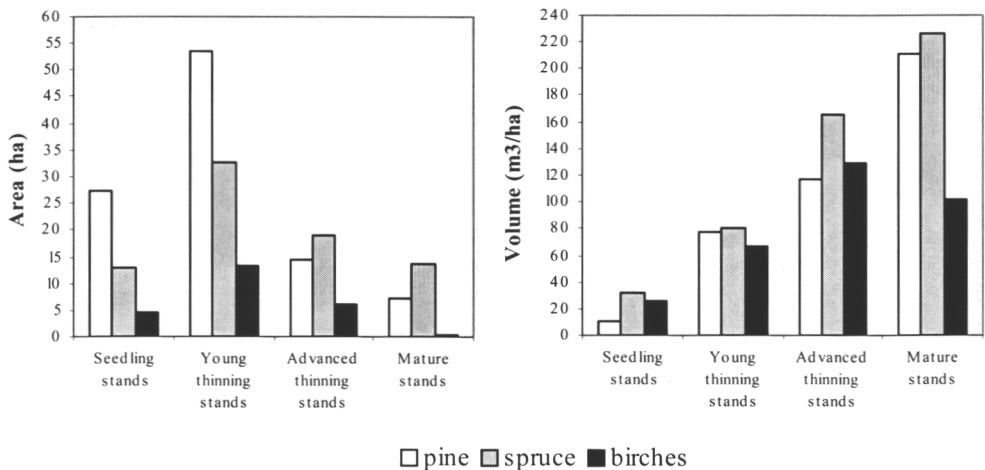

□ pine ▨ spruce ■ birches

Figure 19. The area and the volume of different development classes by dominant tree species in the study data.

In MELA simulations the calculation period of 50 years was divided into five sub-periods of ten years each. The inventories had been made during the years 1998 and 1999, and therefore, the data were first updated to the year 1999. Thus, the calculation period lasted until the end of the year 2049. In the simulations, the built-in assumptions based on the recommendations of Forestry Center Tapio in 2001 for forest management practices were used (see EVENT parameter in Redsven et al. 2004).

In the simulations, the biomass of trees was estimated using both Marklund's (1988) and Hakkila's (1979, 1991) models. When the biomass of trees was applied as a constraint for the optimization task, the optimization was made twice, so that both sets of models were used for the calculation of the constraints.

Four different optimization tasks were designed (Table 15). In task 1, the net present value (NPV) was maximized using an interest rate of 4%. This task represented a typical MELA optimization (e.g. Nuutinen and Hirvelä 2000, 2003), with which the other tasks could be compared. The effect of interest rate was analyzed by using also interest rates of 3% and 5%. These three interest rates are commonly used for the determination of the value of the forests in Finland (Oksanen-Peltola 1994, Nuutinen and Hirvelä 2000, 2003). In task 1, the selected management

schedules were the same irrespective of the set of biomass models, because biomass was not used as a goal or as a constraint. Based on the tree-level comparisons (see chapter 3.2.1, section *'By size of tree'*) the largest differences between the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models were expected on seedling stands and on mature stands.

The purpose of the rest of the tasks was to analyze how the different values of the biomass constraint produced by Marklund's (1988) and Hakkila's (1979, 1991) models affect the selection of the management schedule in the optimization. In task 2, the NPV was maximized using an interest rate of 4% and the biomass of cutting drain had to be set at a higher level than during the preceding sub-period. In task 2, the cutting drain was used instead of cutting removal, because the objective was to compare the effects of the use of different biomass models for the calculation of the biomass constraint, and the division of stem biomass into different timber assortments related to cutting removal would have caused difficulties. In addition, the use of the cutting drain as the constraint corresponded better to the situation in which trees are used for energy production. In task 2, the objective also was to study the influence of demand about increased cutting drain on the carbon sequestration of trees.

In task 3, the NPV was maximized, so that the biomass of the above-ground components of living trees at the end of each sub-period had to be more than at the end of the preceding sub-period. By means of the problem definition used in task 3, the effect of carbon sequestration of trees on the forest management could be considered. The size distributions of living and cut trees are different, and thus, the relative differences of the constraints estimated using different biomass models might also differ in tasks 2 and 3.

In task 4, the goal was the same as in the aforementioned tasks, but the biomass of above-ground components of living trees at the end of each sub-period had to be more than at the end of the preceding sub-period and biomass of cutting drain had to be more than during the preceding sub-period. The aim of task 4 was to study what kind of effect the combination of the constraints used in tasks 2 and 3 had on the selection of the management schedule. Furthermore, the objective was to study how the combination of the simultaneous demand about increasing cutting drain and increasing biomass of trees influences the net carbon sequestration of the trees.

Table 15. Optimization tasks. In each task the biomass of trees was estimated using Marklund's (1988) and Hakkila's (1979, 1991) sets of biomass models. In tasks 2, 3 and 4 the optimization was made twice using both sets of models for the calculation of biomass constraints.

| | GOAL | CONSTRAINTS | |
	Max NPV	Biomass of cutting drain more than during the preceding sub-period	Biomass of living trees at the end of each sub-period more than at the end of the preceding sub-period
Task 1	X		
Task 2	X	X	
Task 3	X		X
Task 4	X	X	X

The solutions of the optimizations were analyzed for each optimization task. First, the effect of different values of the same biomass constraint produced by the chosen sets of models was studied by considering the total cutting area for each of the optimization tasks (Figure 20). The total cutting removal was also compared at the forest area level during the calculation period. In order to find out the significance of the differences, the comparisons of cutting area and cutting removal were made by using the relative differences. In addition, the uniformity of cutting times was checked at the stand level. The management of forest was the same, if the cutting times were also the same.

Second, the management schedules were compared during the sub-periods for each task (Figure 20). The optimal solution for a task may be different because of different value of the constraint estimated by the Marklund's (1988) and Hakkila's (1979, 1991) biomass models. The effects of differences in cutting times, number of cuttings, cutting area and volume of cutting removal were studied for different cutting methods during each sub-period. The studied cutting methods were clear cutting, seeding felling and overstory removal. In this classification the shelterwood felling in spruce was included within seeding felling. Other tending operations included thinning, tending of young stand and clearing of the regeneration area.

Third, the differences in the biomass of trees estimated using both sets of models were studied in various development classes at the beginning of each sub-period. The comparisons between the outputs of the biomass models were made if the optimization produced exactly the same solution irrespective of the model used for determination of the constraint (Figure 20). The relative differences between the outputs of the models in the biomass of single components of trees, and in the biomass of the sum of all above-ground components of trees were studied by development classes at forest area level. The classification of simulation data to different development classes by dominant tree species follows the same guidelines as that of the study data (see pages 81-82).

Finally, the differences in the net carbon sequestration were analyzed for each task at the forest area level. In addition, an attempt was made to identify the general trend concerning the development of the amount of net carbon sequestered by trees at the forest area level during the calculation period using both selected sets of biomass models. The amount of net carbon (NC) sequestered by the above-ground components of the trees was estimated by subtracting the biomass of living trees in the time t1 (m_{t1}) from the biomass of living trees in the time t2 (m_{t2}). The amount of carbon was assumed to be 50% of the biomass of the component (Eq. 9) (see Karjalainen et al. 1994, Nurmi 1997).
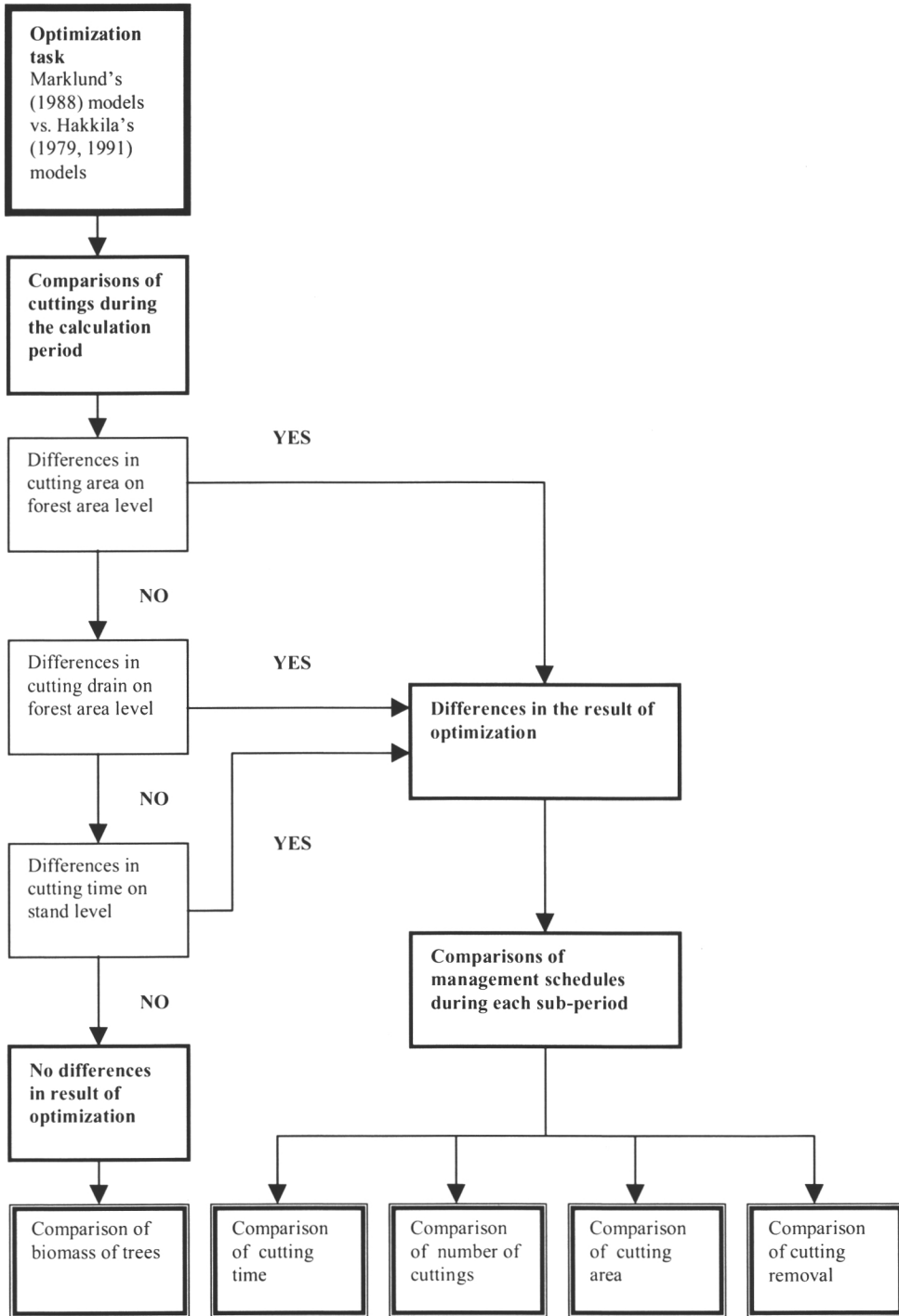
Figure 20. Study of differences in the management schedules caused by different values of constraints estimated by Marklund's (1988) and Hakkila's (1979, 1991) biomass models inside each task.

$$NC = (m_{t2} - m_{t1}) * 0.5 \tag{9}$$

The carbon was assumed to be released immediately to the atmosphere when a tree died. Thus, the slow decay of dead wood was not taken into account. The cut trees were assumed to be taken away from the forest immediately after cutting. The reasons for the differences in carbon balance of trees during the calculation period were studied by comparing the volume of increment and that of total removal in tasks 2, 3 and 4 to those in task 1.

3.3.3 Results from the selection of management schedules

The use of Marklund's (1988) or Hakkila's (1979, 1991) functions for the calculation of biomass constraints in the tasks 2-4 caused small differences in the net present values (Table 16). The differences were the largest in task 4.

Table 16. Net present values (interest rate 4%) (€) in different optimization tasks in 1999-2049.

	1999	2009	2019	2029	2039	2049
Task 1	699 030	700 362	846 719	987 627	1 064 040	917 213
Task 2						
- Marklund (1988)	699 000	701 985	836 559	991 920	1 062 924	916 575
- Hakkila (1979, 1991)	698 999	702 020	836 556	991 916	1 062 917	916 575
Task 3						
- Marklund (1988)	698 432	700 629	845 834	984 077	1 032 354	1 093 574
- Hakkila (1979, 1991)	698 472	700 689	845 922	984 208	1 026 908	1 084 339
Task 4						
- Marklund (1988)	698 199	702 304	840 733	979 152	1 064 792	1 124 251
- Hakkila (1979, 1991)	698 280	702 293	840 936	982 376	1 062 188	1 119 428

In task 1, a rise in interest rate increased the total cutting removal during the calculation period. The increase in cutting removal was very strong when the interest rate was increased from 3% to 4%, and it was more moderate when the rate was raised from 4% to 5%. The rise of interest rate increased cuttings in the first subperiod. The increase of interest rate reduces the profitability of forestry, and therefore, the optimal rotation period is decreased and the forests are thinned earlier (Pukkala 1994). Because biomass of trees was not determined as an objective or constraints in the optimization in task 1, the management of the stands was exactly the same independent of the used set of biomass models.

For task 2, the use of different biomass models for the estimation of values of constraints in optimization caused only minimal differences in cutting area (difference was so small, that it cannot be seen in Figure 21), and also in cutting removal (Figure 22). In this task, as in all other tasks having biomass as a constraint, the cutting removal was a little larger during the calculation period, when the constraint was estimated using Hakkila's (1979, 1991) biomass models. The management of the stands was similar excluding one stand (1.17 ha), in which the area was divided slightly differently between two management schedules.
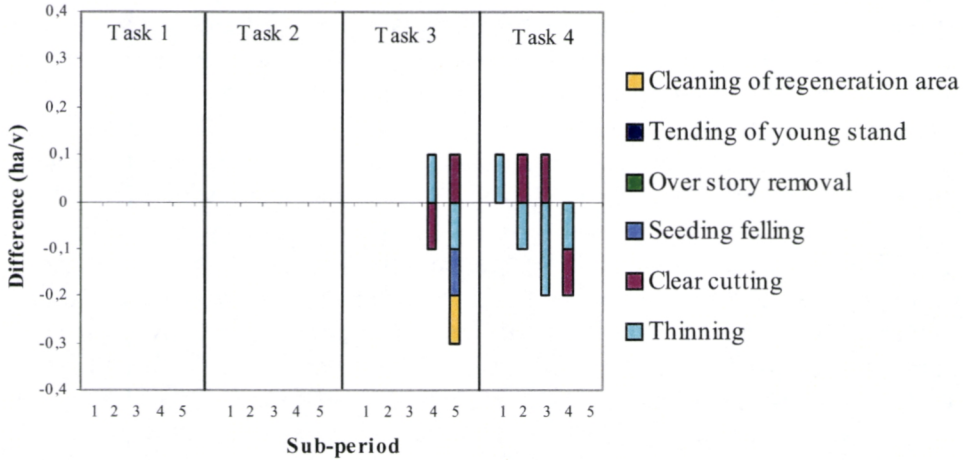
Figure 21. Absolute differences in the cutting area by cutting method in each optimization task during the sub-periods. The positive values mean that the optimizations having the constraint estimated using Marklund's (1988) biomass models produced larger cutting areas than those having the constraint estimated using Hakkila's (1979, 1991) models. The negative values mean that the use of Hakkila's (1979, 1991) models as the constraint resulted in larger cutting areas.
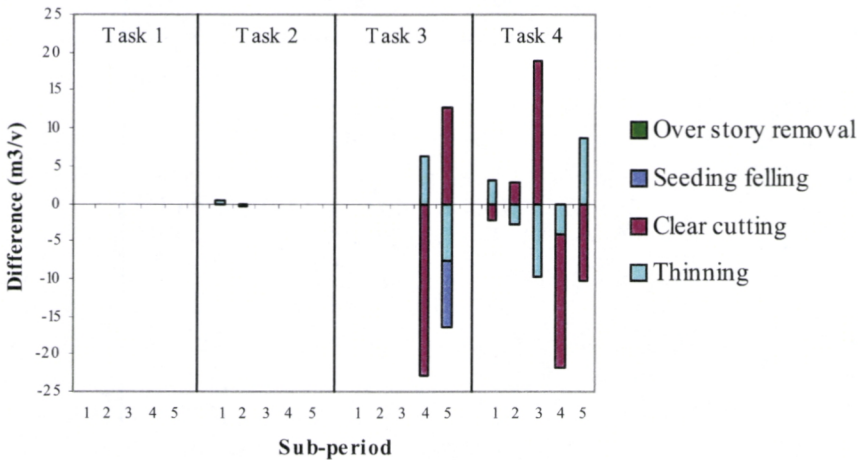
Figure 22. Absolute differences in the cutting removal by cutting method in each optimization task during the sub-periods. The positive values mean that the optimizations having the constraint estimated using Marklund's (1988) biomass models produced larger cutting removals than those having the constraint estimated using Hakkila's (1979, 1991) models. The negative values mean that the use of Hakkila's (1979, 1991) models as the constraint resulted in larger cutting removals.

Although both the number and timing of commercial cuttings were the same irrespective of the models used for the calculations of the constraint for task 3, there were small differences in cutting areas and cutting removal of three stands (total 7.4 ha). Both the cutting area and the cutting removal differed by less than 1% during the calculation period. The use of the outputs of Hakkila's (1979, 1991) models as a constraint produced larger thinning and clear-cutting areas and larger cutting removals both from thinnings and clear cuttings than Marklund's (1988) models. On two stands the reason for differences was the same as in task 1; the area of both stands was divided differently between two management schedules in the optimization. In addition, on one stand the different value of the constraint had an effect on the regeneration felling method at one point of time. When the constraint was calculated using Hakkila's (1979, 1991) models, one clear cutting was replaced by a seeding felling of pine during the fifth sub-period.

Within task 3, the biggest differences in the forest management could be seen during the last two sub-periods (Figures 21 and 22). The differences in thinning area and in the volume of cutting removal from thinnings were, however, less than 2% during both of these periods (Table 17). During the fourth sub-period, the use of Marklund's (1988) models for the estimation of the constraint produced larger thinning area and larger volume of cutting removal from thinnings than the use of Hakkila's (1979, 1991) models. During the fifth sub-period the results were the opposite. The differences in the volume of cutting removal from thinnings were due to the differences in cutting area.

For task 3, both the clear cutting area and the volume of cutting removal from clear cuttings differed by 7% at the highest during the two last sub-periods because of different values of the constraint in the optimization. During the fourth sub-period the clear cutting area was larger and the volume of cutting removal was larger, when the constraint was calculated using Hakkila's (1979, 1991) models (Figures 21 and 22). During the fifth sub-period the use of the outputs of Marklund's (1988) models as the constraint gave a larger clear cutting area and larger cutting removal (Table 17). During the fourth sub-period the reason for differences was the differences in the cutting area. During the fifth sub-period the cutting removal per hectare was also higher when Marklund's (1988) models were applied in the optimization. The reason for this was that seeding felling was made on one stand instead of clear cutting, when the constraint was estimated using Hakkila's (1979, 1991) models.

Also within task 4 the difference was less than 1% between the biomass models with respect to cutting area and to cutting removal during the calculation period. The management of stands differed on eight stands (total 9.63 ha). As was the case for other tasks, for task 4 Hakkila's (1979, 1991) models produced larger thinning and clear-cutting areas and larger cutting removals from thinnings and from clear cuttings during the calculation period.

For task 4 the number of thinnings was greater and on average thinnings were made a little earlier when the constraint was estimated using Hakkila's (1979, 1991) models. The area of thinnings and the volume of cutting removal from thinnings were larger during the second, third and fourth periods when the constraint was determined using Hakkila's (1979, 1991) models (Figures 21 and 22). During the first and the fifth sub-periods the use of Marklund's (1988) models gave a lar-

ger cutting removal and during the first sub-period larger cutting area from thin-nings. The differences were less than 3% both in thinning area and the volume of cutting removal from thinnings during each of these sub-periods (Table 17). The differences in cutting removal from thinnings were mainly due to differences in cutting area, although also the mean intensity of cuttings (m^3/ha) varied during the sub-periods.

Table 17. Relative differences in number of cuttings, cutting areas and cutting removals during the sub-periods. The differences were classified as follows: white <1%; light blue 1-5%; yellow 6-10%; orange 11-15%; red >15%. M = Marklund's (1988) models produced larger values, H = Hakkila's (1979, 1991) models produced larger values.

Sub-period	TASK 1 Marklund vs. Hakkila					TASK 2 Marklund vs. Hakkila					TASK 3 Marklund vs. Hakkila					TASK 4 Marklund vs. Hakkila				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
NUMBER OF CUTTINGS																				
- tending of young stands																				H
- thinnings														H					H	M
- seeding fellings														H						
- over story removal																				
- clear cuttings														M	H	M	M	H		
- cleaning of regeneration areas														H						H
CUTTING AREA, ha																				
- tending of young stands																				
- thinnings														M	H	M	H	H	H	
- seeding fellings															H					
- over story removal																				
- clear cuttings														H	M		M	M	H	
- cleaning of regeneration areas															H					
CUTTING REMOVAL, m³																				
- thinnings														M	H	M	H	H	H	M
- seeding fellings															H					
- over story removal																				
- clear cuttings														H	M		M	M	H	H

The number of regeneration felling was the same within task 4 during the calculation period, but they were made at different times. The average regeneration felling time was, however, the same. The area of clear cuttings differed most during the second, the third and the fourth sub-periods for task 4 (Figure 21). The optimization, in which the constraint was estimated using Marklund's (1988) models gave 13-14% larger area of clear cuttings during the second and the third sub-periods (Table 17). During the fourth sub-period the optimization, in which the constraint was estimated by Hakkila's (1979, 1991) models produced 5% larger area of clear cuttings. During the third sub-period the cutting removal from clear cuttings was 10% greater, and during the fourth and the fifth sub-periods 6-7% smaller, when the constraint was estimated using Marklund's (1988) models. Within this task, the main reasons for the different volume of cutting removal from clear cuttings during the sub-periods were the different cutting areas and intensities of cuttings, which were due to different timings of cuttings.

In summary, the estimates of the constraints produced by Marklund's (1988) or Hakkila's (1979, 1991) biomass models caused some small differences for the selection of the management schedules inside the same optimization task. Generally, in the studied area the constraint estimated by Marklund's (1988) models restricted the size of cutting area and the amount of cutting removal more than the constraint estimated by Hakkila's (1979, 1991) models during the calculation period. The differences in the forest management were greatest for task 4; this was because task 4 had the strictest constraint concerning the biomass. In task 4 the constraint was the combination of task 2 and task 3. The differences were larger for task 3 than for task 2. The different size-distribution of cut and living trees had an effect on the difference in the optimization results between and within these tasks. It might have been expected that there would be larger differences in the forest management within task 2, because the biomass estimates for cut trees were supposed to differ considerably from each other. The reason for this was assumed to be the smaller amount of cut trees, which would have increased the relative amount of random error in the biomass estimates of cut trees.

In this case study, the structure of data had a great effect on the optimization results. It was not needed to restrict the cutting removal very much, because the forest area was dominated by young thinning stands at the initial stage, and thus, the cuttings were postponed to the future. If the initial data had been more dominated by the mature stands, the selection of the management schedules would have been expected to differ more. In addition, the sum of the biomass of the above-ground components was used for the calculation of the constraint, and therefore, the values of constraint do not differ much from each other. If the constraint would have been determined using only different components of crown, the differences might have been more considerable.

The amount of difference in the selection of the management schedules caused by the use of the different set of biomass models for the estimation of a constraint depends also on the determination of the optimization task. When the constraint was determined as the difference between the sequential sub-periods, the management schedules were rather similar because the models gave rather consistent results for the differences between diameter classes. If the biomass constraint would

be given as the certain target level, the management schedules could differ much more from each other.

3.3.4 Results from biomass and net carbon sequestration of trees during the calculation period

The comparisons of the biomass of the above-ground components of the trees estimated by Marklund's (1988) and Hakkila's (1979, 1991) models in the different development classes were made only for task 1 because for other tasks the results of optimization differed due to the different value of the biomass constraint. In task 1 the biomass of living trees estimated using Marklund's (1988) models were generally larger than those calculated by Hakkila's (1979, 1991) models in all development classes (Figure 23). However, at the end of the fifth sub-period (year
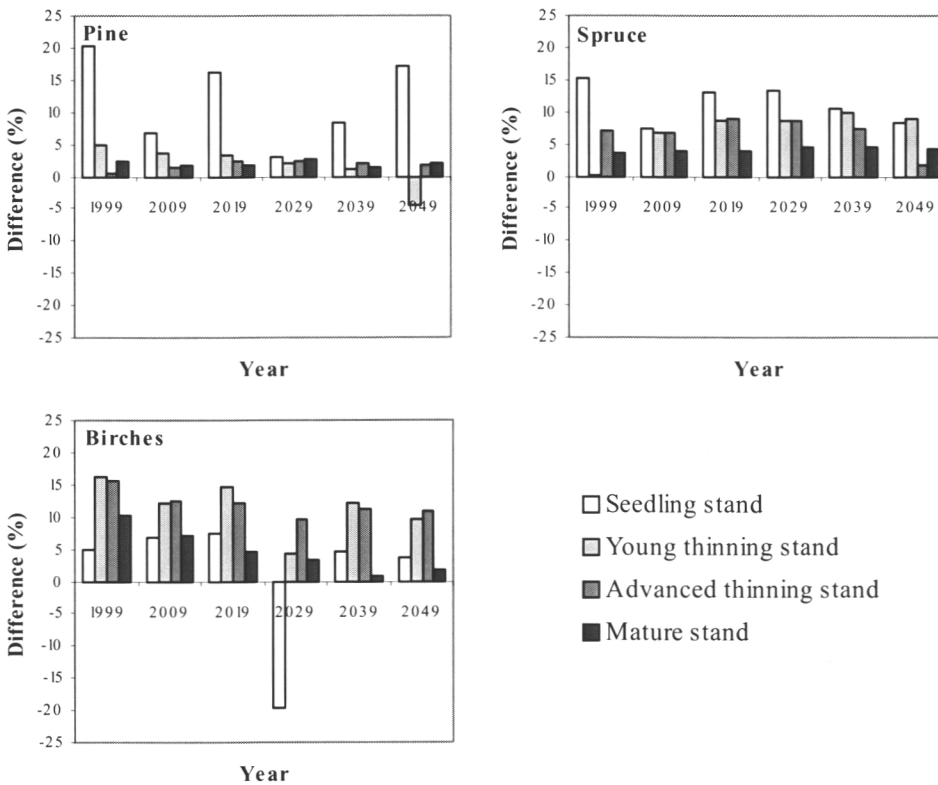
Figure 23. The differences in the biomass of the sum of the above-ground components of trees estimated by Marklund's (1988) and Hakkila's (1979, 1991) models in different development classes in task 1. The positive differences mean that Marklund's (1988) models produced larger values for biomass. The negative differences mean that Hakkila's (1979, 1991) models produced larger values for biomass.

2049) the biomass of trees in pine-dominated young thinning stands was larger, and at the end of the third sub-period (year 2029) the biomass of trees in birch-dominated seedling stands was larger, when Hakkila's (1979, 1991) models were used for the biomass estimations. Excluding seedling stands the differences between the sum of the outputs of the models for the above-ground components of the trees were less than or equal to 5% in pine stands and less than 10% in spruce stands. In birch stands the differences were larger, but less than 17% in all development classes apart from seedling stands.

For single components of trees, Marklund's (1988) models produced larger estimates than Hakkila's (1979, 1991) models at the end of most of the sub-periods. The differences between the outputs of the models for stem wood, living branches and foliage of all tree species and dead branches of pine and spruce were more than 20% in seedling stands at the end of several sub-periods. The difference between the outputs of the models for living branches was also large in young thinning and advanced thinning stands of spruce and birch, and mature stands of birch at the end of some sub-periods. The outputs for foliage differed between Marklund's (1988) and Hakkila's (1991) models mostly, in addition to seedling stands, in young thinning stands and mature stands of spruce. The differences in the biomass of dead branches were more than 20% in seedling, young thinning and mature stands of all tree species and in advanced thinning stands of birch. Otherwise the differences between the outputs of Marklund's (1988) and Hakkila's (1979) models for single components of a tree were less than 20%.

The results corresponded to the studies made at tree level (see Table 12). The correspondence between the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models at stand level depends on the proportional distribution of tree species and on diameter and height distributions of trees. The differences between the models were the largest for birch at tree level, and thus, the biomass estimates may differ most in birch-dominated stands. The wide diameter range, in which the models correspond to each other at tree level, means that the stand-level considerations of biomass of trees are also probably close to each other. The differences in the estimates of Marklund's (1988) and Hakkila's (1979, 1991) biomass models for single components of trees appear easily in young thinning stands and in mature stands. In young thinning stands the relative amount of small trees, for which the models produce the largest differences, is usually great compared to other development classes. Although in mature stands Hakkila's (1979, 1991) models resulted in unrealistically high estimates for some components (see Figure 4), Marklund's (1988) models produced larger values for the biomass of above-ground components in mature stands. Generally, the number of very thick trees is small in mature stands, and thus, they have not very large effect on the total biomass. In this study the problem was that on seedling stands it was not possible to estimate biomass for all small trees, or at least for all components of a tree, using the considered models. The trees or components of trees having zero value for biomass vary depending on the model, and this partly explained the large differences between Marklund's (1988) and Hakkila's (1979, 1991) models for seedling stands.

In task 1 the absolute differences in the biomass estimates of trees were the highest at the end of the second sub-period. They were the largest in advanced thinning stands dominated by spruce, where Marklund's (1988) models gave much

larger estimates than Hakkila's (1979, 1991) models. The situation was also the same in advanced thinning stands of birch at the end of the second sub-period. The reason for these differences was that compared to other points of time, the volume of trees in advanced thinning stands dominated by spruce or birches was large at the end of the second sub-period. Thus, at the forest area level the differences between the outputs of the models depend greatly on stand structure.

In each task, the differences between the outputs of Marklund's (1988) and Hakkila's (1979, 1991) models in the net carbon sequestered by the trees were the largest at the end of the second sub-period (year 2019) (Figure 24). The net carbon sequestered by the trees was 186-206 Mg larger when the net carbon was estimated using Marklund's (1988) models. The relative differences were 22-25% at the end of that sub-period (Table 18). The main reason for the differences was the large amount of the tree biomass in the advanced thinning stands, especially in the advanced thinning stands of spruce, which caused large absolute differences. Mainly, for the same reason the absolute differences were high also at the end of the next sub-period. At the end of the third sub-period, the outputs of Hakkila's (1979, 1991) models for the net carbon sequestered by the trees were 90-127 Mg larger than those of Marklund's (1988) models. The relative difference varied from 9% to 16%. The relative differences were 12-15% at the end of the fourth sub-period, and the absolute difference was rather high at the end of the fifth sub-period in tasks 1 and 2. In these two tasks the net carbon sequestration of the trees was larger at the end of the fifth sub-period, when Hakkila's (1979, 1991) models were used for the estimation of the biomass. The absolute differences were mainly due to the large amount of the biomass in advanced thinning and mature stands of spruce. Although the amount of biomass was also larger in the pine-dominated thinning stands, it did not have a great effect on the absolute differences between the models in the net carbon sequestered by trees in tasks 1 and 2 at the end of the fifth sub-period. In task 4 the relative difference was high at the end of the fifth sub-period, but the absolute difference was small.

Table 18. The relative differences in the net carbon sequestered by trees in each task during the sub-periods. The differences were classified as follows: white <1%; light blue 1-5%; yellow 6-10%; orange 11-15%; red >15%. M = Marklund's (1988) models produced larger values, H = Hakkila's (1979, 1991) models produced larger values.

	TASK 1 Marklund vs. Hakkila					TASK 2 Marklund vs. Hakkila					TASK 3 Marklund vs. Hakkila					TASK 4 Marklund vs. Hakkila				
Sub-period	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Net carbon sequestrated by trees	H	M	H	H	H		M	H	H	H		M	H				M	H	M	H

The general trend in the net carbon sequestered by the trees was derived using the outputs of both Marklund's (1988) and Hakkila's (1979, 1991) models. In task 1 the net carbon sequestration of trees excluding stumps and roots was positive and amounted to 740-950 Mg at the end of the first three sub-periods (years 2009-2029) on the studied forest area (Figure 24). The amount of net carbon was also positive at the end of the fourth sub-period (year 2039), but not as much as at the end of the former periods. At the end of the last sub-period (year 2049) there was a net release of carbon which amounted to more 1600 Mg. In task 1 the increment increased during the calculation period until the end of the fourth sub-period. During the fifth sub-period increment decreased due to intensive cuttings. The cutting
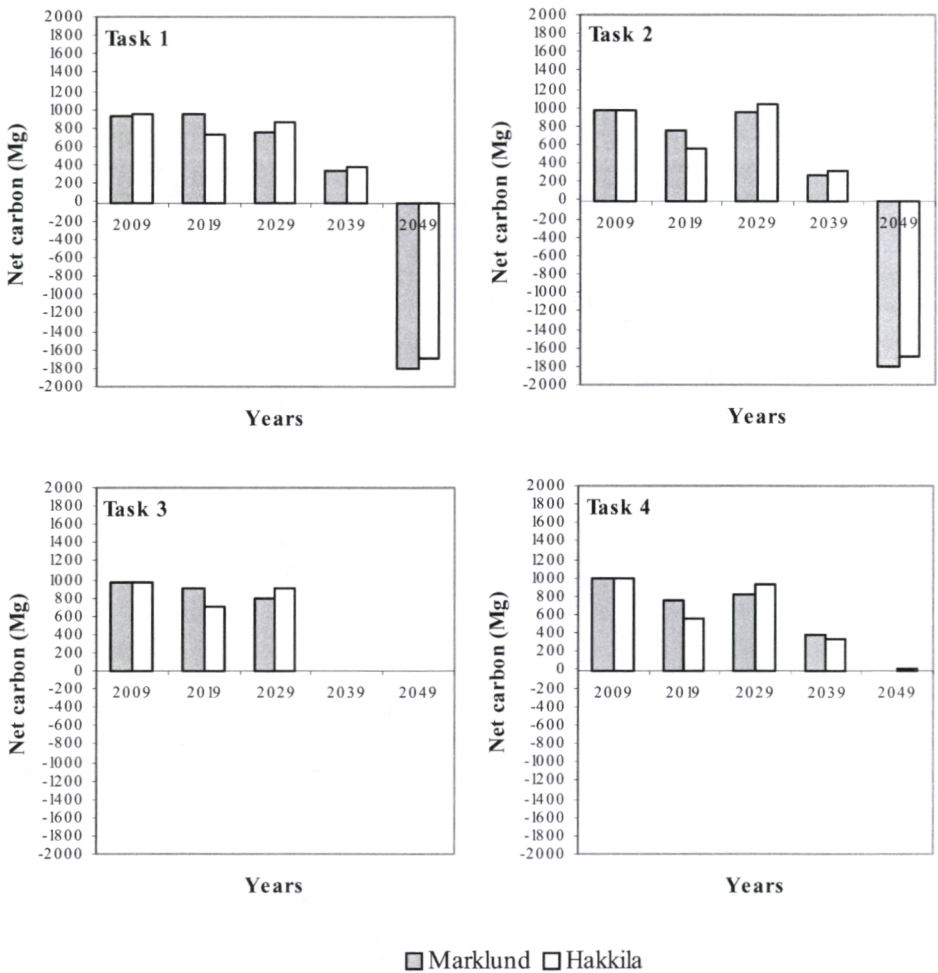
Figure 24. Net carbon sequestered by trees in each optimization task during the calculation period.

removal was smaller during the second sub-period than during the first sub-period, and after that it increased strongly. The cutting removal from thinnings was the largest during three last sub-periods and that from regeneration felling during the first and the last sub-period. The cutting removal exceeded the increment only during the last sub-period.

In task 2 the net carbon sequestered by trees was smaller at the end of the second sub-period (year 2019) and larger at the end of the third sub-period (year 2029) than the net carbon sequestration of trees in task 1 (Figure 24). The main reasons for these differences were the larger cutting removal from thinnings during the second sub-period, and the smaller cutting removal during the third sub-period in task 2. The total cutting removal was a little smaller in task 2 than in task 1 during the whole calculation period.

When the net carbon sequestered by trees in task 3 was compared to that sequestered by trees in task 1, there were only small differences at the end of three first sub-periods (years 2009-2029) (Figure 24). In task 3 the total cutting removal was almost as big as the increment during the fourth and the fifth sub-periods, for which the amount of net carbon was very close to zero.

In task 4 the net carbon sequestered by trees was much smaller than in task 1 at the end of the second sub-period (year 2019) (Figure 24); the main reason for this was the larger cutting removal from thinnings in task 4. In task 4 the amount of net carbon was about zero at the end of the last sub-period, which was due to larger increment and smaller cutting removal compared to task 1.

4 CONCLUSIONS

In this study, the applicability of available biomass models for the use in the forestry modeling and analyses was evaluated. The models were aimed at estimating the total biomass of above-ground components, and the biomass of different components of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), silver birch (*Betula pendula)* and downy birch (*B. pubescens*) growing on different sites throughout Finland. The evaluation was carried out in the context of the planning system MELA, which is widely used in Finland for supporting the decision making in forestry. However, the results of this study are also applicable in the context of other forest planning systems in which the tree-level models can be used for the estimation of the biomass.

In this study, statistical tests cannot be used for the evaluation of biomass models because of the lack of representative empirical data. Therefore, the performance of the most representative biomass models was assessed by analyzing the structure of modeling data, the capability of models to describe different components of a tree, and the capability of used independent variables to describe different components of a tree. This evaluation showed that the models developed by Marklund (1988) for Sweden, and Hakkila (1979, 1991) for Finland were the most promising from the candidate models (Appendices 4-8) for the biomass calculation in forestry modeling and analyses. In the more detailed evaluation, the outputs of selected Marklund's (1988) models were compared to those of selected Hakkila's (1979)

models on different sites (fertile or infertile, and mineral soils or peatlands) and geographical locations (Northern or Southern Finland). The evaluation also included the study of these functions as regards the input and output of the models in the context of the MELA planning system. The evaluation as a whole made it possible to identify the special features of the model performance, with an increase in understanding of how the models functioned at different levels of application (tree, stand, forest area). Based on the evaluation, the gaps in knowledge were identified in order to direct future studies. It was also possible to identify the uncertainties in model calculations that were due to the poorly identified model structure and exclusion of important processes.

Marklund's (1988) models proved to be more applicable than Hakkila's (1979, 1991) models for the estimation of biomass of different components of trees. The data behind Marklund's (1988) models were the most representative compared with other models available for biomass calculations at the tree level. The data were collected from Sweden, where the range of growing conditions is wider than in Finland. Therefore, the variability in the data also covered the variation of the site conditions and structure of tree populations in Finland. In spite of the wider range of growing conditions included into Marklund's (1988) data, based on comparisons between the outputs of Marklund's (1988) and Hakkila's (1979, 1991), Marklund's (1988) models are applicable also in Finland. The models for the different biomass components were mostly derived from the same set of sample trees of pine and spruce, except for the finest fraction of roots. Furthermore, Marklund (1988) formulated models for different components of birch excluding stump, roots and leaves. From Marklund's (1988) models for the biomass of above-ground components of pine and spruce, it was possible to obtain full sets having both breast height diameter and height as independent variables. For the living branches of birch, Marklund (1988) did not present models having both breast height diameter and height as independent variables. However, for other above-ground components of birch, Marklund (1988) had models having both of these variables as independent variables.

Marklund's (1988) models provided acceptable estimates for the biomass of different components of trees over the whole diameter range regardless of the species; i.e. the functions do not produce negative values for the smallest trees and the biomass of the largest diameter trees are reasonable. When the biomass is estimated for an individual component of a tree, the models are the most applicable for the estimation of the biomass of the stem wood and the biomass of stem bark. When the total above-ground biomass in trees is considered, the models are the most applicable for regularly managed stands dominated by Scots pine. The modeling data and the input data used in this study were collected mostly from regularly managed stands. Furthermore, the sums of the outputs of Marklund's (1988) models for above-ground components of pines corresponded well with the outputs of Hakkila's (1979, 1991) models. The most extensive comparisons with other studies were possible for pine. The sum of the outputs for above-ground components of pine were also in line with these previous studies. The analysis done in this study showed that Marklund's (1988) models produce logical outputs for the total above-ground biomass of trees all over Finland.

When Marklund's (1988) models are used for the estimation of biomass at smaller than the country level, attention has to be paid to the location and the structure of forest area (e.g. site fertilities, proportion of different development classes). When the biomass is used as a goal or a constraint in the optimization in a forest planning system, the location and the structure of forest area also affects the reliability of the optimization result. The models produce the more uncertain outputs, the more the structure of input data deviate from the data used for the formulation of the models. For example, the estimation of biomass for trees growing in Northern Finland (or in Southern Finland) produces more biased estimates than the estimation of tree biomass over the whole country. Based on this study, no conclusions about the amount of biases in different forest areas can be drawn. However, it can be concluded, that the performance of models in terms of the biomass of stem wood and stem bark is realistic as regards the location and the fertility of site.

As a conclusion, Marklund's (1988) models are not directly applicable for the estimation of energy wood resources. Energy wood consists mostly of living branches. The reliability of biomass estimates for living branches depend greatly on the structure of forests. Thus, at the regional level the estimates can be very unreliable. In Finland, at the country level only very coarse estimates about energy wood resources can be made using Marklund's (1988) models. Marklund's (1988) models are more applicable for the estimation of carbon sequestration of the above-ground components of trees than for the estimation of energy wood resources. The proportion of stem wood is the largest in the biomass of above-ground components of a tree. Therefore, the outputs of Marklund's (1988) models for the total biomass of above-ground components are more reliable than those for single components of a crown. In addition to country level, Marklund's (1988) models produce realistic estimates for the biomass of above-ground components of trees at the regional level.

In the future more attention should be paid to the development of more realistic biomass models. The models should be able to account for the characteristics of the variability of the input data. In a forest planning system used for the estimation of forest resources at different regional levels, the models should be able to describe the special features of trees at all levels. For resolutions smaller than the country level, this demand requires the formulation of different models (or calibration of the models) for different sites in different parts of the country. When the trees having different sizes are considered, the main interest in the modeling should be to increase the accuracy of the most common diameter classes; however, the models should also produce reasonable outputs for the smaller and larger diameter classes. In order to guarantee the compatibility of different models (e.g. volume and biomass) in a forest planning system, they should be derived from the same data.

In this study, the methods were represented for the systematization of the evaluation of the set of biomass models for different components of a tree. The evaluation of the set of models for different components of a tree demanded a versatile study of the models in relation to each other. The methods used in this study were based on more efficient utilization of existing data and research results than usually have been made in the evaluation of the models. Although the statistical tests would not be possible for the evaluation of the models, this study showed that

useful information about the performance of the models could be obtained using other evaluation methods.

References

Albrektson, A. 1980. Tallens biomassa. Storlek – utveckling - uppskattningmetoder. *Biomass of Scots pine (Pinus sylvestris L.). Amount – development – methods of mensuration.* The Swedish University of Agricultural Sciences. Department of Silviculture. Report no. 2. 189 p.

- 1988. Needle Litterfall in Stands of *Pinus sylvestris* L. in Sweden, in Relation to Site Quality, Stand Age and Latitude. Scandinavian Journal of Forest Research 3: 333-342.

Asikainen, A., Ranta, T., Laitila, J. and Hämäläinen, J. 2001. Hakkuutähdehakkeen kustannustekijät ja suurimittakaavainen hankinta. Research Notes 131. University of Joensuu, Faculty of Forestry. 107 p.

Baskerville, G. L. 1965. Estimation of dry weight of tree components and total standing crop in conifer stands. Ecology, Volume 46, Issue 6: 867-869.

Bergstedt, A. and Olesen, P. O. 2000. Models for Predicting Dry Matter Content of Norway Spruce. Scandinavian Journal of Forest Research 15: 633-644.

Björklund, T. 1984. Tervalepän biomassa. *Biomass of black alder.* The Finnish Forest Research Institute, Research Papers 151. 71 p.

- and Ferm, A. 1982. Pienikokoisen koivun ja harmaalepän biomassa ja tekniset ominaisuudet. *Biomass and technical properties of small-sized birch and grey alder.* Folia Forestalia 500. 37 p.

Bray, J. R. and Gorham, E. 1964. Litter production in forests of the world. Advances in ecological research, Volume 2. Academic Press, London: 101-157.

Buchman, R. G. and Shifley, S. R. 1983. Guide to evaluating forest growth projection systems. Journal of Forestry 81: 232-234, 254.

Cale, W. G. Jr., O'Neill, R. V. and Shugart, H. H. 1983. Development and application of desirable ecological models. Ecological Modelling 18: 171-186.

Castrén, T. and Simula, M. 2000. Hiilen sitomisen edistäminen. In: Sieppi, S. (ed.). Ympäristönsuojelun vuosikirja. Saha- ja levyteollisuus. Vuoden 1999 tilastot. Metsäteollisuus ry. 56 p.

Caswell, H. 1976. The validation problem. In: Shugart, H. H. and O'Neill, R. V. 1979. Systems Ecology. Benchmark Papers in Ecology/9. Dowden, Hutchinson & Ross, Inc: 296-308.

Chatfield, C. 1995. Model uncertainty, data mining and statistical inference. Journal of the Royal Statistical Society. Series A, Volume 158, No. 3: 419-466.

Chertov, O. C., Komarov, A. S. and Karev, G. P. 1999. Modern approaches in forest ecosystem modelling. European Forest Institute Research Report 8. 116 p.

Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A.M., Trexler, M. C. and Wisniewski, J. 1994. Carbon pools and fluxes of global forest ecosystems. Science, Volume 263: 185-190.

Ericsson, E. 2003. Carbon accumulation and fossil fuel substitution during different rotation scenarios. Scandinavian Journal of Forest Research 18: 269-278.

Ferm, A. 1990. Nuorten vesasyntyisten hieskoivikoiden kehitys ja lahoisuus turvemaalla. *Development and decay of young Betula pubescens coppice stands on peatland.* Folia Forestalia 744. 17 p.

- and Kaunisto, S. 1983. Luontaisesti syntyneiden koivumetsiköiden maanpäällinen lehdetön biomassatuotos entisellä turpeennostoalueella Kihniön Aitonevalla. *Above-ground leafless biomass production of naturally generated birch stands in a peat-over area at Aitoneva, Kihniö.* Folia Forestalia 558. 32 p.

Field measurement procedures for carbon accounting. Bush for greenhouse. 2002. Report no 2 – version 1. Australian Greenhouse Office. 22 p. Available from http://www.greenhouse.gov.au/bfg/field-measurement/index.html. [updated 18 November 2002; cited 23 September 2003].

Finér, L. 1989. Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire. Acta Forestalia Fennica 208. 63 p.

- 1991. Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog. Acta Forestalia Fennica 223. 42 p.

Finnish Statistical Yearbook of Forestry 2003. SVT Agriculture, forestry and fishery 2003:45. Finnish Forest Research Institute. 385 p.

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

Hakkila, P. 1966. Investigations on the basic density of Finnish pine, spruce and birch wood. Communicationes Instituti Forestalis Fenniae 61.5. 98 p.

- 1967. Vaihtelumalleja kuoren painosta ja painoprosentista. *Variation patterns of bark weight and bark percentage by weight.* Communicationes Instituti Forestalis Fenniae 62.5. 37 p.

- 1968. Geographical variation of some properties of pine and spruce pulpwood in Finland. Communicationes Instituti Forestalis Fenniae 66.8. 59 p.

- 1969. Weight and composition of the branches of large Scots pine and Norway spruce trees. Communicationes Instituti Forestalis Fenniae 67.6. 37 p.

- 1970. Basic density, bark percentage and dry matter content of grey alder (*Alnus incana*). Communicationes Instituti Forestalis Fenniae 71.5. 33 p.

- 1971. Coniferous branches as a raw material source. A sub-project of the joint Nordic research programme for the utilization of logging residues. Communicationes Instituti Forestalis Fenniae 75.1. 60 p.

- 1972a. Mechanized harvesting of stumps and roots. A sub-project of the joint Nordic research programme for the utilization of logging residues. Communicationes Instituti Forestalis Fenniae 77.1. 71 p.

- 1972b. Oksaraaka-aineen korjuumahdollisuuden Suomessa. *Possibilities of harvesting branch raw material in Finland.* Folia Forestalia 159. 19 p.

- 1976. Kantopuu metsäteollisuuden raaka-aineena. *Stumpwood as industrial raw material.* Folia Forestalia 292. 39 p.

- 1979. Wood density survey and dry weight tables for pine, spruce and birch stems in Finland. Communicationes Instituti Forestalis Fenniae 96.3. 59 p.

- 1989. Utilization of Residual Forest Biomass. Springer-Verlag. 568 p.

- 1991. Hakkuupoistuman latvusmassa. *Crown mass of trees at the harvesting phase.* Folia Forestalia 773. 24 p.

- 2002. Puutavara. In: Väätäjä, M. (ed.). Matkalle tehtaalle. Puutavaran kaukokuljetuksen ja tehdasvastaanoton vaiheita: 46-52.

- and Uusvaara, O. 1968. On the basic density of plantation-grown Norway spruce. Communicationes Instituti Forestalis Fenniae 66.6. 22 p.

- , Laasasenaho, J. and Oittinen, K. 1972. Korjuuteknisiä oksatietoja. *Branch data for logging work.* Folia Forestalia 147. 15 p.

- , Kalaja, H. and Mäkelä, M. 1975. Kokopuunkäyttö pienpuuongelman ratkaisuna. *Full-tree utilization as a solution to the problem of small-sized trees.* Folia Forestalia 240. 78 p.

- , Kalaja, H., Salakari, M. and Valonen, P. 1978. Whole-tree harvesting in the early thinning of pine. Folia Forestalia 333. 58 p.

- , Kalaja, H. and Saranpää, P. 1995. Etelä-Suomen ensiharvennusmänniköt kuitu- ja energialähteenä. The Finnish Forest Research Institute, Research Papers 582. 99 p.

Harkin, Z. and Bull, G. 2000. Towards developing a comprehensive carbon accounting framework for forests in British Columbia. Interim Report IR-00-046. IIASA. 62 p.

Hasenauer, H. 2001. Concepts within forest ecosystem modeling and their application. 2°Simpósio Latino-americano sobre Manejo Florestal. 13 e 14 de setembro de 2001. Universidade Federal de Santa Maria. Centro de Ciências Rurais. Programa de pós-graduacão em engenharia florestal: 39-54.

Heiskanen, V. 1957. Raudus- ja hieskoivun laatu eri kasvupaikoilla. *Quality of the common birch and the white birch on different sites.* Communicationes Instituti Forestalis Fenniae 48.6. 99 p.

- and Rikkonen, P. 1976. Havusahatukkien kuoren määrä ja siihen vaikuttavat tekijät. *Bark amount in coniferous sawlogs and factors affecting it.* Folia Forestalia 250. 31 p.

Hildén, M., Kuuluvainen, J., Ollikainen, M., Pelkonen, P. and Primmer, E. 1999. Kansallisen metsäohjelman ympäristövaikutusten arviointi. Asiantuntijaryhmän loppuraporttiteksti 17.9.1999. Ministry of Agriculture and Forestry. 76 p. Available from http://www.mmm.fi/kmo/asiakirjat_raportit/pdf/kmoyva.pdf. [updated 17 June 2004; cited 4 August 2004].

Hocker, H. W. Jr. 1979. Introduction to Forest Biology. John Wiley & Sons. 467 p.

Hoen, H. F. and Solberg, B. 1994. Potential and Economic Efficiency of Carbon sequestration in Forest Biomass Through Silvicultural Management. Forest Science, Volume 40, No. 3: 429-451.

Hynynen, J. 1987. Metsäpuiden juuristojen rakenne. Kirjallisuuteen perustuva tutkimus. University of Helsinki. Department of silviculture. Research notes N:o 61. 111 p.

- 2001. Energiapuuvarat. In: Nurmi, J. and Kokko, A. Biomassan tehostetun talteenoton seurannaisvaikutukset metsässä. The Finnish Forest Research Institute, Research Papers 816: 9-16.

- Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H. and Haapala, P. 2002. Models for predicting stand development in MELA system. The Finnish Forest Research Institute, Research Papers 835. 116 p.

Ilvessalo, Y. 1965. Metsänarvioiminen. 400 p.

- 1969. Luonnonnormaalien metsiköiden kehityksestä Pohjanmaan kivennäis-mailla. *On the development of Natural Normal Forest Stands on Mineral Soils in Ostrobothnia.* Acta Forestalia Fennica 96. 37 p.

Issakainen, A. 1988. Männyn, kuusen ja koivun juurakoiden biomassa ja ravinteet ojitetulla suolla. Helsingin yliopisto, suometsätieteen laitos. Tutkielma MMK-tutkintoa varten. 68 p.

Kangas, A. 2001a. Mallien käyttö. In: Maltamo, M. and Laukkanen, S. (eds.). Metsää kuvaavat mallit. Silva Carelica 36. University of Joensuu, Faculty of Forestry: 223-239.

- 2001b. Tilastollinen malli. In: Maltamo, M. and Laukkanen, S. (eds.). Metsää kuvaavat mallit. Silva Carelica 36. University of Joensuu, Faculty of Forestry: 1-29.

- and Kangas, J. 1999. Optimization bias in forest management planning soulutions due to errors in forest variables. Silva Fennica 33(4): 303-315.

Karjalainen, T. and Kellomäki, S. 1996. Greenhouse gas inventory for land use change and forestry in Finland based on international guidelines. Mitigation and Adaptation Strategies for Global Change 1: 51-71.

- , Kellomäki, S. and Pussinen, A. 1994. Role of wood-based products in absorbing atmospheric carbon. Silva Fennica 28(2): 67-80.

Kärkkäinen, M. 1985. Puutiede. 415 p.

Kauppi, P., Tomppo, E. and Ferm, A. 1995. C and N storage in living trees within Finland since 1950s. Plant and Soil 168-169: 633-638.

Keller, M., Palaceb, M. and Hurttb, G. 2001. Biomass estimation in the Tapajos National Forest, Brazil. Examinations of sampling and allometric uncertainties. Forest Ecology and Management, Volume 154, Issue 3: 371-382.

Kellomäki, S. and Väisänen, H. 1986. Kasvatustiheyden ja kasvupaikan viljavuuden vaikutus puiden oksikkuuteen taimikko- ja riukuvaiheen männiköissä. Summary: *Effect of stand density and site fertility on the branchiness of Scots pines at pole stage.* Communicationes Instituti Forestalis Fenniae 139. 38 p.

- , Lämsä, P., Oker-Blom, P. and Uusvaara, O. 1992. Männyn laatukasvatus. Silva Carelica 23. University of Joensuu. 133 p.

Knowe, S. A., Ahrens, G. R. and DeBell, D. S. 1997. Comparison of diameter-distribution, stand-table-projection, and individual-tree-growth modeling approaches for young red alder plantations. Forest Ecology and Management 98: 49-60.

Koivisto, P. 1972. Kainuun ja Pohjanmaan talousmänniköiden kehityksestä. *On the development of Scots pine stands in Central Finland.* 19 p.

Korhonen, K. T. and Maltamo, M. 1990. Männyn maanpäällisten osien kuivamassat Etelä-Suomessa. The Finnish Forest Research Institute, Research Papers 371. 29 p.

Kubin, E. 1982. Karike ja sen merkityksestä metsänhoidossa. In: Metsäntutkimuspäivä Oulaisissa 1982. The Finnish Forest Research Institute, Research Papers 70: 30-39.

Kuuluvainen, T. 1988. Crown architecture and stem wood production in Norway spruce (*Picea abies (L.) Karst.*) Tree Physiology 4: 337-346.

Laasasenaho, J. 1982. Taper curve and volume functions for pine, spruce and birch. Communicationes Instituti Forestalis Fenniae 108. 74 p.

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: 1-53.

Lämsä, P., Kellomäki, S. ja Väisänen, H. 1990. Nuorten mäntyjen oksikkuuden riippuvuus puuston rakenteesta ja kasvupaikan viljavuudesta. *Branchiness of young Scots pines as related to stand structure and site fertility.* Folia Forestalia 746. 22 p.

Lappi, J. 1992. JLP: A Linear Programming Package for Management Planning. The Finnish Forest Research Institute, Research Paper 414. 134 p.

Leary, R. A. 1997. Testing models of unthinned red pine plantation dynamics using a modified Bakuzis matrix of stand properties. Ecological Modelling 98: 35-46.

Lehtonen, A., Mäkipää, R., Heikkinen, J., Sievänen, R. and Liski, J. 2004. Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. Forest Ecology and Management 188: 211-224.

Liski, J., Pussinen, A., Pingoud, K., Mäkipää, R. and Karjalainen, T. 2001. Which rotation length is favourable to carbon sequestration? Canadian Journal of Forest Research 31: 2004-2013.

Losi, C. J., Siccama, T. G., Condit, R. and Morales, J. E. 2003. Analysis of alternative methods for estimating carbon stock in young tropical plantations. Forest Ecology and Management 184: 355-368.

Lounais-Suomen metsäkeskus. 2001. Lounais-Suomen metsäohjelma 2001-2005. 103 p.

Maa- ja metsätalousministeriö. 1999. Kansallinen metsäohjelma 2010. MMM:n julkaisuja 2/1999. 38 p.

Mäkelä, A. and Vanninen, P. 1998. Impacts of size and competition on tree form and distribution of aboveground biomass in Scots pine. Canadian Journal of Forest Research 28: 216-227.

- Mäkinen, H., Vanninen, P., Hynynen, J., Kantola, A. and Mielikäinen, K. 2000. Männiköiden tuotoksen ja laadun ennustaminen. The Finnish Forest Research Institute, Research Papers 794. 89 p.

Mäkipää, R., Karjalainen, T., Pussinen, A. and Kellomäki, S. 1999. Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone. Canadian Journal of Forest Research 29: 1490-1501.

Malinen, J. and Pesonen, M. 1996. Etelä-Suomen energiapuuvarat. The Finnish Forest Research Institute, Research Papers 610. 33 p.

- Pesonen, M., Määttä, T. and Kajanus, M. 2001. Potential harvest for wood fuels (energy wood) from logging residues and first thinnings in Southern Finland. Biomass and Bioenergy 20: 189-196.

Mälkönen, E. 1972. Hakkuutähteiden talteenoton vaikutus männikön ravinnevaroihin. *Effect of harvesting logging residues on the nutrient status on Scotch pine stands.* Folia Forestalia 157. 14 p.

- 1977. Annual primary production and nutrient cycle in a birch stand. Communicationes Instituti Forestalis Fenniae 91.5. 35 p.

- and Saarsalmi, A. 1982. Hieskoivikon biomassatuotos ja ravinteiden menetys kokopuun korjuussa. *Biomass production and nutrient removal in whole tree harvesting of birch stands.* Folia Forestalia 534. 17 p.

Mankin, J. B., O'Neill, R. V., Shugart, H. H. and Rust, B. W. 1979. The importance of validation in ecosystem analysis. In: Shugart, H. H. and O'Neill, R. V. Systems Ecology. Benchmark Papers in Ecology/9. Dowden, Hutchinson & Ross, Inc: 309-317.

Marklund, L. G. 1987. Biomass functions for Norway spruce (*Picea abies* (L.) Karst.) in Sweden. Swedish University of Agricultural Sciences. Department of Forest Survey. Report 43. 127 p.

- 1988. Biomassafunktioner för tall, gran och björk i Sverige. Swedish University of Agricultural Sciences. Department of Forest Survey. Report 45. 73 p.

Marttila, V., Granholm, H., Heikinheimo, P., Hyvärinen, E., Joutsamo, E., Karjalainen, T., Kauppi, P., Kortelainen, P., Mäkipää, R., Nuutinen, T., Nyrhinen, T., Pingoud, K., Raivio, S., Esala, M. and Tomppo, E. 2000. Metsät ilmastosopimuksessa ja Kioton pöytäkirjassa. Ministry of Agriculture and Forestry. Publication 1/2000. 88 p.

Mattila, E. and Keskimölö, A. 1994. Energiapuun korjuumahdollisuuksien arviointi metsän hakkuu- ja hoitoehdotusten perusteella. Rovaniemen energiapuukertymäarvio 1984-93. The Finnish Forest Research Institute, Research Papers 534. 52 p.

Mayer, D. G. and Butler, D. G. 1993. Statistical validation. Ecological Modelling 68: 21-32.

Metsätalouden kehittämiskeskus Tapio. 2001. Hyvän metsänhoidon suositukset. 95 p.

Mielikäinen, K., Hirvelä, H., Härkönen, K. and Malinen, J. 1995. Energiapuu osana metsänkasvatusta Keski-Pohjanmaalla. The Finnish Forest Research Institute, Research Papers 556. 56 p.

Mikkelä, H., Sampo, S. and Kaipainen, J. (eds.). 2000. Suomen metsätalouden tila 2000. Kestävän metsätalouden kriteerit ja indikaattorit. Ministry of Agriculture and Forestry. Publication 5/2000. 104 p.

Minkkinen, K., Laine, J. and Hökkä, H. 2001. Tree Stand Development and Carbon Sequestration in Drained Peatland Stands in Finland – a Simulation Study. Silva Fennica 35(1): 55-69.

Niinemets, Ü, Ellsworth, D. S., Lukjanova, A. and Tobias, M. 2001. Site fertility and the morphological and photosynthetic acclimation of *Pinus sylvestris* needles to light. Tree Physiology 21: 1231-1244.

Nikinmaa, E., Kaipiainen, L., Mäkinen, M., Ross, J. and Sasonova, T. 1996. Geographical Variation in the Regularities of Woody Structure and Water Transport. In: Hari, P., Ross, J. and Mecke, M. (ed.) Production Process of Scots Pine; Geographical Variation and Models. Acta Forestalia Fennica 254: 49-78.

Nurmi, J. 1997. Heating values of mature trees. Acta Forestalia Fennica 256. 28 p.

Nuutinen, T. and Hirvelä, H. 2000. Valtakunnan metsien 9. inventointiin perustuvat hakkuumahdollisuusarviot vuosille 1998-2027 Lounais-Suomen metsäkeskuksen alueella. Metsätieteen aikakauskirja 2B/2000: 413-428.

- and Hirvelä, H. 2003. Valtakunnan metsien 9. inventoitiin perustuvat hakkuumahdollisuusarviot vuosille 2001-2030 Kainuun metsäkeskuksen alueella. Metsätieteen aikakauskirja 2B/2003: 257-272.

- and Kellomäki, S. 2001. A comparison of three modelling approaches for large-scale forest scenario analysis in Finland. Silva Fennica 35(3): 299-308.

Nylinder, M. 1980. Projekt helträdsutnyttjande – några reflektioner. In: Albrektson, A., Lindroth, S. and Stömne, P-E. (ed.). Nordisk Biomassaforskning. Symposium i Umeå 23-25 oktober 1979. Swedish University of Agricultural Sciences. Department of Forest Survey. Report 29: 113-120.

Oderwald, R. G. and Hans, R. P. 1993. Corroborating models with model properties. Forest Ecology and Management 62: 271-283.

Oksanen-Peltola, L. 1994. Metsän arvon määrittäminen. In: Tapion taskukirja. 22. uudistettu painos. Kustannusosakeyhtiö Metsälehti, Helsinki: 403-428.

Oliver, C. D. 1992. Similarities of stand structures and stand development processes throughout the world – some evidence and applications to silviculture through adaptive management. In: Kelty, M. J., Larson, B. C. and Oliver, C. D. (ed.). The Ecology and silviculture of Mixed-Species Forests. Kluwer Academic Publisher: 11-26.

Olsson, M. T. 1978. Undersökningar over bioelement i bark från gran, tall och björk. *Bioelement Studies in Spruce, Pine and Birch Bark.* Reports in Forest Ecology and Forest Soils. Swedish University of Agricultural Sciences. 80 p.

Oreskes, N., Shrader-Frechette, K. and Belitz, K. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science, Volume 263: 641-646.

Östlin, E. 1963a. Barkuppgifter för tall, gran, björk m. fl. Del 1. Barkuppgifter för län, regioner. *Bark Data for Pine, Spruce, Birch, etc. Part 1. Bark Data for Provinces and Regions.* Department of Forest Survey. Royal College of Forestry. Research Notes 5. 146 p.

- 1963b. Barkuppgifter för tall, gran, björk m. fl. Del 2. Barkuppgifter för bonitets- och ålderklasser och för olika sortiment. *Bark Data for Pine, Spruce, Birch, etc. Part 2. Bark Data for Site- and Age-classes and for Sawlogs and Pulpwood.* Department of Forest Survey. Royal College of Forestry. Research Notes 6: 1-67.

Paavilainen, E. 1980. Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. Communicationes Instituti Forestalis Fenniae 98.5. 71 p.

Päivinen, R. 1978. Kapenemis- ja kuorimallit männylle, kuuselle ja koivulle. *Taper and bark thickness models for pine, spruce and birch.* Folia Forestalia 353. 32 p.

Parresol, B. R. 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. Forest Science 45(4): 573-593.

- 2001. Additivity of nonlinear biomass equations. Canadian Journal of Forest Research 31: 865-878.

Petersson, H. 1999. Biomassafunktioner för trädfraktioner av tall, gran och björk i Sverige. Arbetsrapport 59. Sveriges Lantbruksuniversitet. 31 p.

Pietikäinen, J., Vaijärvi, E., Ilvesniemi, H., Fritze, H. and Westman, C. J. 1999. Carbon storage of microbes and roots and the flux of CO_2 across a moisture gradient. Canadian Journal of Forest Research 29: 1197-1203.

Porté, A. and Bartelink, H. H. 2002. Modelling mixed forest growth: a review of models for forest management. Ecological Modelling 150: 141-188.

Power, M. 1993. The predictive validation of ecological and environmental models. Ecological Modelling, 68: 33-50.

Prisley, S. P. and Mortimer, M. J. 2004. A synthesis of literature on evaluation of models for policy applications, with implications for forest carbon accounting. Forest Ecology and Management 198: 89-103.

Pukkala, T. 1994. Metsäsuunnittelun perusteet. 242 p.

Ranta, E., Rita, H. and Kouki, J. 1997. Biometria. Tilastotiedettä ekologeille. Kuudes painos. Yliopistopaino. Helsinki. 569 p.

Rastetter, E. B. 1996. Validating models of ecosystem response to global change. BioScience 46(3): 190-198.

Redsven, V., Anola-Pukkila, A, Haara, A., Hirvelä, H., Härkönen, K., Kettunen, L., Kiiskinen, A., Kärkkäinen, L., Lempinen, R., Muinonen, E., Nuutinen, T., Salminen, O. and Siitonen, M. 2004. MELA2002 Reference Manual (2nd edition). The Finnish Forest Research Institute. 606 p. Available from http://www.metla.fi/metinfo/mela/index.htm. [updated 27 February 2004; cited 4 August 2004].

Reich, P. B., Oleksyn, J. Modrzynski, J. and Tjoelker, M. G. 1996. Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. Tree Physiology 16: 643-647.

Robinson, A. P. and Ek, A. R. 2000. The consequences of hierarchy for modeling in forest ecosystems. Canadian Journal of Forest Research 30: 1837-1846.

Rykiel, E. J. Jr. 1996. Testing ecological models: the meaning of validation. Ecological Modelling 90: 229-244.

Saarsalmi, A. and Mälkönen, E. 1989. Harmaalepikon biomassan tuotos ja ravinteiden käyttö. *Biomass production and nutrient consumption in Alnus incana stands.* Folia Forestalia 728. 16 p.

-    , Palmgren, K. and Levula, T. 1991. Harmaalepän vesojen biomassan tuotos ja ravinteiden käyttö. *Biomass production and nutrient consumption of the sprouts of Alnus incana.* Folia Forestalia 768. 25 p.

-    , Palmgren, K. and Levula, T. 1992. Harmaalepän ja rauduskoivun biomassan tuotos ja ravinteiden käyttö energiapuuviljelmillä. *Biomass production and nutrient consumption of Alnus incana and Betula pendula in energy forestry.* Folia Forestalia 797. 29 p.

Salemaa, M. and Lindgren, M. 1998. Latvuksen kunto. In: Mälkönen, E. (ed.) Ympäristömuutos ja metsien kunto. Metsien terveydentilan tutkimusohjelman loppuraportti. The Finnish Forest Research Institute, Research Papers 691: 103-110.

-    Lindgren, M. and Jukola-Sulonen, E-L. 1995. Neulasmassa ja sen vaihtelu. In: Tikkanen, E. Kuolan saastepäästöt Lapin metsien rasitteena: 123-126.

Schroeder, P. and Ladd, L. 1991. Slowing the increase of atmospheric carbon dioxide: a biological approach. Climate Change 19: 283-290.

Sedjo, R. A. 2000. Ilmastosopimuksen taloudelliset vaikutukset metsäsektorilla. Metsätieteen aikakauskirja 4/2000: 613-616.

Sievänen, R. 2000. Kansallisen ilmasto-ohjelman metsätoimialan taustaselvitys. Maa- ja metsätalousministeriön tilaama muistio. Finnish Forest Research Institute. 32 p.

Siitonen, M. 1993. Experiences in the Use of Forest Management Planning Models. Silva Fennica 27(2): 167-178.

- 1996. MELA ja metsien kehityksen ennustaminen. In: Hynynen, J. and Ojansuu, R. (eds.). Puuston kehityksen ennustaminen – MELA ja vaihtoehtoja. Tutkimusseminaari Vantaalla 1996. The Finnish Forest Research Institute, Research Papers 612: 7-19.

- , Härkönen, K., Hirvelä, H., Jämsä, J., Kilpeläinen, H., Salminen, O. and Teuri, M. 1996. MELA Handbook. 1996 Edition. The Finnish Forest Research Institute, Research Papers 622. 452 p.

Simola, P. 1977. Pienikokoisen lehtipuuston biomassa. *The biomass of small-sized hardwood trees*. Folia Forestalia 302. 16 p.

Sirén, M., Tanttu, V., Siipilehto, J., Aaltio, H. and Mäntynen, E. 2000. Ensiharvennusleimikot metsähakkeen korjuukohteena – PUUT04. In: Alakangas, E. (ed.). Puuenergian teknologiaohjelman vuosikirja 2000. VTT Symposium 205: 69-84.

Snowdon, P., Raison, J., Keith, H., Ritson, P., Grierson, P., Adams, M., Montagu, K., Bi, H., Burrows, W. and Eamus, D. 2002. Protocol for sampling tree and stand biomass. National carbon accounting system. Technical report no. 31. 66 p. Available from http://www.greenhouse.gov.au/ncas/reports/tr31final.html [updated 25 July 2003; cited 13 February 2004].

Soares, P., Tomé, M., Skovsgaard, J. P. and Vanclay, J. K. 1995. Forest Ecology and Management 71: 251-265.

Stage, A. R. 2003. How forest models are connected to reality: evaluation criteria for their use in decision support. Canadian Journal of Forest Research 33: 410-421.

Stakanov, V. D., Alexeyev, V. A. and Korotkov, I. A. 1998. Methods for Evaluating Phytomass and Carbon in Forest Communities. In: Alexeyev, V. A. and Birdsey, R. A. Carbon storage in forests and peatlands of Russia: 24-36.

Turkia, K. and Kellomäki, S. 1987. Kasvupaikan viljavuuden ja puuston tiheyden vaikutus nuorten mäntyjen oksien läpimittaan. *Influence of the site fertility and stand density on the diameter of branches in young Scots pine stands*. Folia Forestalia 705. 16 p.

Uusvaara, O. 1983. Viljelymänniköistä saadun sahatavaran laatu ja arvo. The Finnish Forest Research Institute, Research Papers 122. 105 p.

Valinger, E. 1993. Crown development of Scots pine trees following thinning and nitrogen fertilization. Studia Forestalia Suecica, No. 188. 12 p.

Valtanen, J. 1994. Pohjois-Suomen metsänhoidon erityispiirteet. In: Tapion taskukirja. Kustannusosakeyhtiö Metsälehti: 235-245.

Vanclay, J. K. and Skovsgaard, J. P. 1997. Evaluating forest growth models. Ecological Modelling 98: 1-12.

Vanninen , P., Ylitalo, H., Sievänen, R. and Mäkelä, A. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris L.*). Trees 10: 231-238.

Vesterlin, V. 1996. Energiapuuvarat ja niiden hyödyntämisedellytykset 1/1994-12/1996 – D105. In: Vuosikirja 1995. Osa I. Puupolttoaineiden tuotantotekniikka. Bioenergian tutkimusohjelma. Julkaisuja 11: 75-83.

Voipio, R. and Laakso, T. 1992. Pienikokoisten puiden maanpäällisen biomassan

kemiallinen koostumus. *Chemical composition of the above ground biomass of small-sized trees.* Folia Forestalia 789. 22 p.

Vuokila, Y. and Väliaho, H. 1980. Viljeltyjen havumetsiköiden kasvatusmallit. *Growth and yield models for conifer cultures in Finland.* Communicationes Instituti Forestalis Fenniae 99.2. 271 p.

Appendix 1. The sample tree characteristics of pine in the NFI data. In brackets the sample tree characteristics, when the biomass of stem wood and stem bark was estimated using Hakkila's (1979) models.

SCOTS PINE	n	DIAMETER (cm)				HEIGHT (m)			
		min	max	$\bar{x}$	s	min	max	$\bar{x}$	s
WHOLE FINLAND									
Mineral soils	27106	0.3	70.0	20.7	9.4	1.4	35.2	14.7	5.9
	(17379)	(1.0)	(66.6)	(21.4)	(9.4)	(3.1)	(34.2)	(15.6)	(6.0)
Peatlands	10276	0.7	52.6	15.5	7.3	1.5	28.4	11.0	4.7
	(6025)	(1.6)	(52.6)	(16.5)	(7.3)	(3.1)	(27.4)	(12.0)	(4.7)
Fertile mineral soils	15662	0.4	66.6	22.2	9.6	1.4	35.2	16.0	6.1
	(10716)	(1.8)	(66.6)	(22.8)	(9.6)	(3.1)	(34.2)	(16.8)	(6.1)
Infertile mineral soils	11444	0.3	70.0	18.7	8.7	1.4	31.6	12.9	5.1
	(6663)	(1.0)	(58.0)	(19.1)	(8.5)	(3.1)	(31.6)	(13.7)	(5.2)
SOUTHERN FINLAND									
Mineral soils	19511	0.3	66.6	21.4	9.5	1.4	35.2	15.7	6.1
	(16328)	(1.0)	(66.6)	(21.6)	(9.4)	(3.1)	(34.2)	(15.8)	(6.0)
Peatlands	6772	0.7	52.6	16.6	7.5	1.5	28.4	12.2	4.9
	(5590)	(1.6)	(52.6)	(16.7)	(7.4)	(3.1)	(27.4)	(12.3)	(4.7)
NORTHERN FINLAND									
Mineral soils	7595	0.6	70.0	18.9	8.8	1.4	26.4	12.3	4.7
	(1051)	(2.6)	(57.5)	(18.7)	(8.9)	(3.1)	(25.3)	(12.1)	(4.6)
Peatlands	3504	0.7	43.3	13.3	6.3	1.5	24.0	8.7	3.5
	(435)	(2.0)	(33.1)	(13.8)	(6.3)	(3.1)	(19.2)	(8.8)	(3.4)

Appendix 2. The sample tree characteristics of spruce in the NFI data. In brackets the sample tree characteristics, when the biomass of stem wood and stem bark was estimated using Hakkila's (1979) models.

NORWAY SPRUCE	n	DIAMETER (cm)				HEIGHT (m)			
		min	max	$\bar{x}$	s	min	max	$\bar{x}$	s
WHOLE FINLAND									
Mineral soils	21410	0.5	63.1	21.0	9.7	1.4	35.4	16.2	6.4
	(15425)	(2.3)	(62.4)	(21.6)	(9.6)	(3.1)	(35.4)	(16.9)	(6.3)
Peatlands	4690	0.8	52.6	17.7	8.9	1.5	32.6	13.6	6.2
	(3091)	(2.7)	(52.6)	(18.8)	(8.8)	(3.1)	(31.6)	(14.7)	(6.0)
Fertile mineral soils	20192	0.5	63.1	21.3	9.6	1.4	35.4	16.5	6.4
	(14764)	(2.3)	(62.4)	(21.9)	(9.6)	(3.1)	(35.4)	(17.2)	(6.2)
Infertile mineral soils	1218	1.2	49.2	15.5	8.4	1.8	29.1	11.0	5.0
	(661)	(3.0)	(49.2)	(15.1)	(7.9)	(3.1)	(29.1)	(11.5)	(5.1)
SOUTHERN FINLAND									
Mineral soils	18071	0.5	63.1	21.5	9.8	1.4	35.4	16.9	6.4
	(15018)	(2.3)	(62.4)	(21.7)	(9.6)	(3.1)	(35.4)	(17.0)	(6.3)
Peatlands	3601	0.8	52.6	18.6	9.1	1.5	32.6	14.7	6.2
	(2955)	(2.7)	(52.6)	(19.0)	(8.9)	(3.1)	(31.6)	(14.9)	(6.0)
NORTHERN FINLAND									
Mineral soils	3339	1.1	53.5	18.3	8.6	1.5	27.0	12.3	4.9
	(407)	(3.6)	(42.6)	(18.8)	(7.7)	(3.1)	(23.7)	(12.7)	(4.6)
Peatlands	1089	1.3	45.6	14.6	7.5	1.7	27.5	10.0	4.7
	(136)	(3.4)	(45.6)	(14.7)	(7.1)	(3.1)	(20.8)	(9.9)	(4.2)

Appendix 3. The sample tree characteristics of birches in the NFI data. In brackets the sample tree characteristics, when the biomass of stem wood and stem bark was estimated using Hakkila's (1979) models.

SILVER AND DOWNY BIRCH	n	DIAMETER (cm)				HEIGHT (m)			
		min	max	x̄	s	min	max	x̄	s
WHOLE FINLAND									
Mineral soils	8927	0.2	62.8	15.7	9.4	1.4	36.5	14.0	6.5
	(5970)	(0.4)	(62.8)	(16.7)	(9.8)	(1.4)	(36.5)	(15.1)	(6.6)
Peatlands	5348	0.3	48.9	11.8	6.7	1.6	27.5	11.1	4.9
	(3208)	(0.3)	(48.9)	(12.6)	(7.1)	(1.6)	(27.5)	(12.0)	(5.1)
Fertile mineral soils	7820	0.2	62.8	16.4	9.5	1.4	36.5	14.6	6.5
	(5377)	(0.4)	(62.8)	(17.3)	(9.8)	(1.4)	(36.5)	(15.6)	(6.5)
Infertile mineral soils	1107	0.3	45.5	11.2	7.4	1.4	28.5	9.4	4.9
	(593)	(0.7)	(45.5)	(11.7)	(8.3)	(1.7)	(28.5)	(10.4)	(5.4)
SOUTHERN FINLAND									
Mineral soils	6711	0.2	62.8	17.0	9.8	1.4	36.5	15.4	6.5
	(5663)	(0.4)	(62.8)	(17.1)	(9.8)	(1.4)	(36.5)	(15.5)	(6.5)
Peatlands	3544	0.3	48.9	12.6	7.1	1.6	27.5	12.3	5.1
	(2972)	(0.3)	(48.9)	(12.8)	(7.1)	(1.6)	(27.5)	(12.3)	(5.1)
NORTHERN FINLAND									
Mineral soils	2216	0.3	40.4	12.0	7.2	1.4	24.5	9.6	4.3
	(307)	(0.4)	(37.2)	(10.7)	(7.4)	(1.7)	(19.0)	(8.6)	(4.0)
Peatlands	1804	0.4	35.2	10.2	5.6	1.7	22.1	8.9	3.5
	(236)	(0.8)	(34.3)	(9.8)	(5.9)	(2.2)	(17.2)	(8.6)	(3.3)

Appendix 4. Marklund's (1988) biomass functions. The biomass is expressed in ln(kilograms). See the explanations of the symbols from the pages 9-10.

Dependent variable	Model	R	s_{res}
Scots Pine			
ln(stem wood)	11.4219*(d/(d+14))-2.2184	0.983	0.300
	7.6066*(d/(d+14))+0.02*h+0.8658*ln(h)-2.6864	0.993	0.191
ln(stem bark)	8.8489*(d/(d+16))-2.9748	0.964	0.339
	7.2482*(d/(d+16))+0.4487*ln(h)-3.2765	0.967	0.326
ln(living branches	9.1015*(d/(d+10))-2.8604	0.949	0.517
incl. needles)	13.3955*(d/(d+10))-1.1955*ln(h)-2.5413	0.960	0.456
ln(needles)	7.7681*(d/(d+7))-3.7983	0.917	0.574
	12.1095*(d/(d+7))+0.0413*h-1.565*ln(h)-3.4781	0.930	0.527
ln(dead branches)	9.5938*(d/(d+10))-5.3338	0.861	0.956
	7.1270*(d/(d+10))-0.0465*h+1.1060*ln(h)-5.8926	0.865	0.945
ln(stump)	11.0481*(d/(d+15))-3.9657	0.972	0.415
ln(roots ≥ 5cm)	13.2902*(d/(d+9))-6.3413	0.943	0.556
ln(roots < 5 cm)	8.8795*(d/(d+10))-3.8375	0.949	0.472
Norway spruce			
ln(stem wood)	11.4873*(d/(d+14))-2.2471	0.991	0.243
	7.2309*(d/(d+14))+0.0355*h+0.703*ln(h)-2.3032	0.996	0.154
ln(stem bark)	9.8364*(d/(d+15))-3.3912	0.983	0.287
	8.3089*(d/(d+15))+0.0147*h+0.2295*ln(h)-3.402	0.984	0.279
ln(living branches	8.5242*(d/(d+13))-1.2804	0.972	0.387
incl. needles)	10.9708*(d/(d+13))-0.0124*h-0.4923*ln(h)-1.2063	0.974	0.374
ln(needles)	7.8171*(d/(d+12))-1.9602	0.948	0.500
	9.7809*(d/(d+12))-0.4873*ln(h)-1.8551	0.949	0.494
	8.4127*(d/(d+12))-1.5628*ln(h)+1.4032*ln(l_c)-1.5732)	0.967	0.398
ln(dead branches)	9.9550*(d/(d+18))-4.3308	0.845	1.094
	3.6518*(d/(d+18))+0.0493*h+1.0129*ln(h)-4.6351)	0.854	1.065
	5.6333*(d/(d+18))+2.7826*ln(h)-1.7460*ln(l_c)-5.3924	0.873	1.001
ln(stump)	10.6686*(d/(d+17))-3.3645	0.979	0.397
ln(roots ≥ 5 cm)	13.3703*(d/(d+8))-6.3851	0.970	0.440
ln(roots < 5 cm)	7.6283*(d/(d+12))-2.5706	0.962	0.416
Silver and downy birch			
ln(stem wood)	10.8109*(d/(d+11))-2.3327	0.985	0.245
	8.1184*(d/(d+11))+0.9783*ln(h)-3.3045	0.995	0.146
ln(stem bark)	10.3876*(d/(d+14))-3.2518	0.973	0.317
	8.3019*(d/(d+14))+0.7433*ln(h)-4.0778	0.979	0.279
ln(living branches excl. leaves)	10.2806*(d/(d+10))-3.3633	0.961	0.531
ln(dead branches)	7.9266*(d/(d+5))-5.9507	0.778	1.182
	11.2872*(d/(d+30))-0.3081*h+2.6821*ln(h)-6.6237	0.788	1.162

Appendix 5. Hakkila's (1972a, 1979, 1991) biomass functions. The dry mass of a stem wood could be estimated by multiplying basic density and green volume. Hakkila's (1972a) functions for stump and roots were converted into formula, in which breast height diameter was used as an independent variable instead of stump diameter (see Hakkila (1972a)). The biomass is expressed in kilograms or ln(kilograms). See the explanations of the symbols from the pages 9-10.

Dependent variable	Model	R^2	s_{res}
Scots pine			
Over bark stem (2.5-7.4 m)	$(-27.43*(d/t)^2+62.44*\ln(h/d)-26.88*\ln(h/t)+0.526*h+381.63)*0.99*V$		
Stem wood (2.5-7.4 m)	$(-27.43*(d/t)^2+62.44*\ln(h/d)-26.88*\ln(h/t)+0.526*h+381.63)*1.01*V_{bl}$		
Over bark stem (> 7.4 m)	$(92.930*(h/d)-193.00*(h/t)^2+1.832*(t/h)+341.77)*0.99*V_{bl}$		
Stem wood (> 7.4 m)	$(92.930*(h/d)-193.00*(h/t)^2+1.832*(t/h)+341.77)*1.01*V_{bl}$		
ln(living branches incl. needles)	$2.3268*\ln(d*10)-9.3954$	0.878	0.427
	$3.4914*\ln(d*10)-1.9498*\ln(h*10)-47.454*(d*10)/(h*10)^2-5.2678$	0.908	0.370
ln(needles)	$1.6975*\ln(d*10)-7.47$	0.688	0.514
	$1.8485*\ln(d*10)+0.0155*cr-9.01$	0.732	0.477
Dead branches	$0.0194*(d*10)-0.84$	0.228	2.46
Stump and roots	$0.044*(d/0.7604)^2-4.9$		
Norway spruce			
Over bark stem (2.5-7.4 m)	$(-67.35*\ln(d/t)-0.270*t+0.001679*h^3+167.7/t-9.837*V^2+17.79*(d/t)^3+307.21)*1.01*V$		
Stem wood (2.5-7.4 m)	$(-67.35*\ln(d/t)-0.270*t+0.001679*h^3+167.7/t-9.837*V^2+17.79*(d/t)^3+307.21)*1.01*V_{bl}$		
Over bark stem (> 7.4 m)	$(-67.95*\ln(d/t)-0.2795*t+0.619*h+19.13*(d/t)^3+303.37)*1.01*V$		
Stem wood (>7.4 m)	$(-67.95*\ln(d/t)-0.2795*t+0.619*h+19.13*(d/t)^3+303.37)*1.01*V_{bl}$		
Living branches incl. needles	$0.10229*(d*10)+3.30*10^{-6}*(d*10)^3-3.71$	0.881	11.73
	$0.00026724*(d*10)^2+1.41*10^{-6}*(d*10)^3+0.00043562*((d*10)^3/(h*10))+0.4112$	0.893	11.14
ln(living branches incl. needles)	$2.3031*\ln(d*10)+0.017075*cr+992.36/(h*10)^2-9.821$	0.923	0.282
ln(needles)	$2.2204*\ln(d*10)-9.03$	0.715	0.513
Needles	$1.592*10^{-8}*(d*10)^3*cr+4.73*10^{-6}*(d*10)*cr^2+0.37$	0.883	4.14
Dead branches	$0.0134*(d*10)+3.9*10^{-8}*(d*10)^3-0.62$	0.266	1.89
Stump and roots	$0.060*(d/0.7411)^2-7.1$		
Silver and downy birch			
Over bark stem (2.5-7.4 m)	$(22.84*\ln(t)+2.771*(t/d)+379.99)*1.015*V$		
Stem wood (2.5-7.4 m)	$(22.84*\ln(t)+2.771*(t/d)+379.99)*1.01*V_{bl}$		
Over bark stem (> 7.4 m)	$(34.156*\ln(t)+138.5/d+335.64)*1.015*V$		
Stem wood (> 7.4 m)	$(34.156*\ln(t)+138.5/d+335.64)*1.01*V_{bl}$		
ln(living branches excl. leaves)	$2.6016*\ln(d*10)-10.7699$	0.839	0.451
	$2.73067*\ln(d*10)+1788.90/(h*10)^2+0.01664*cr-12.4606$	0.886	0.366
Dead branches	$0.0040*(d*10)-0.07$	0.020	1.63

Appendix 6. Korhonen and Maltamo's (1990) biomass functions. The biomass is expressed in ln(kilograms). See the explanations of the symbols from the pages 9-10.

Dependent variable	Model	R^2	s_{res}
Scots pine			
ln(stem wood)	$0.879*\ln(d^2)+1.215*\ln(h)-4.182$	0,992	0.145
	$0.842*\ln(d^2)+1.212*\ln(h)+0.087*\ln(t_b)-4.326$		0.139
ln(stem bark)	$0.885*\ln(d^2)+0.435*\ln(h)-4.344$	0,981	0.168
	$0.905*\ln(d^2)+0.3925*\ln(h)+0.101*CT-4.409$		0.161
ln(living branches incl. needles)	$3.1287*\ln(d)-1.3936*\ln(h)-0.0005298*d^2+0.1162*l_c-3.0599$	0,947	0.303

Appendix 7. Finér's (1989,1991) and Issakainen's (1988) biomass functions for trees growing on peatlands. The biomass of stem wood, stem bark and stump and roots is expressed in ln(kilograms). The biomass of other components is expressed as ln(grams). See the explanations of the symbols from the pages 9-10.

Dependent variable	Site	Model	R^2	s_{res}
Scots pine				
ln(stem wood)	VNRmu	1.8136*ln(d)+0.9317*ln(h-1.3)-3.2875	0.996	0.094
	RhNRmu	2.1064*ln(d)-1.6475	0.962	0.160
	IR	1.7256*ln(d)+1.0241*ln(h*10)-5.7103	0.99	0.064
ln(stem bark)	VNRmu	2.0023*ln(d)-4.0168	0.972	0.175
	RhNRmu	1.6874*ln(d)-2.9847	0.906	0.208
	IR	2.1274*ln(d)-0.7392*ln(h*10)-0.7220	0.97	0.133
ln(living branches excl. needles)	VNRmu	2.2387*ln(d)+3.2988	0.980	0.165
	RhNRmu	3.0560*ln(d)	0.999	0.344
	IR	2.6708*ln(d)+1.3568*ln(cr)+2.7932	0.97	0.224
ln(needles)	VNRmu	(1.8121*ln(d)+2.3958)+(1.6660*ln(d)+3.0319)+ (1.7205*ln(d)+2.8450)		
	RhNRmu	(2.0091*ln(d)+1.1906)+(1.8809*ln(d)+1.8862)+ (1.8666*ln(d)+2.1337)		
	IR	(1.9320*ln(d)+1.1458*ln(cr)+2.8966)+(1.9828* ln(d)+1.1520*ln(cr)+2.6514)+(1.8779*ln(d)+0.8357* ln(cr)+2.6905)		
ln(dead branches)	VNRmu	1.7067*ln(d)+2.9225	0.665	0.620
	RhNRmu	2.7189*ln(d)	0.997	0.424
	IR	2.2181*ln(d)+1.8943	0.87	0.365
ln(stump and roots)	VNRmu, RhNRmu	2.7929*ln(d)-4.5698	0.989	
	IR	2.4142*ln(d)-3.3420	0.99	0.118
Norway spruce				
ln(stem wood)	MKmu	1.5541*ln(d)+1.056*ln(h-1.3)-2.8414	0.998	0.082
ln(stem bark)	MKmu	2.7644*ln(d)-5.9120	0.988	0.191
ln(living branches excl. needles)	MKmu	2.0822*ln(d)+0.6252*ln(cr)+4.1857	0.987	0.180
ln(needles)	MKmu	(1.8981*ln(d)+0.8337*ln(cr)+2.2939)+(1.7137*ln(d) +0.5291*ln(cr)+2.8349)+(1.6714*ln(d)+0.5235* ln(cr)+2.7760)+(1.7820*ln(d)+0.6142*ln(cr)+ 2.5818)+(1.7122*ln(d)+0.5289*ln(cr)+2.4523)+ (1.8232*ln(d)+0.7358*ln(cr)+2.1302+(1.8118*ln(d)+ 1.2274*ln(cr)+3.1615)		
ln(dead branches)	MKmu	0.1328*d+5.5372	0.828	0.665
ln(stump and roots)	MKmu	3.0333*ln(d)-4.9853	0.982	
Silver and downy birch				
ln(stem wood)	RhNRmu	2.3811*ln(d)-2.3362	0.986	0.109
ln(stem bark)	RhNRmu	2.7731*ln(d)-5.5507	0.962	0.213
ln(living branches excl. leaves)	RhNRmu	3.3891*ln(d)	0.999	0.252
ln(leaves)	RhNRmu	2.9749*ln(d)	0.999	0.270
ln(dead branches)	RhNRmu	5.9290*ln(d)-10.9833*ln(cr)-19.7244	0.529	1.901
ln(stump and roots)	RhNRmu	3.0861*ln(d)-5.3806	0.991	

Appendix 8. Laiho's (1997) biomass models for trees growing on peatlands. The biomass is expressed as grams. See the explanations of the symbols from the pages 9-10.

Dependent variable	Model	R^2	s_{res}
Scots pine			
Stem wood	$14.422*d^{1.840}*h^{1.185}$	0.996	4.26
Stem bark	$5.658*d^{2.251}*h^{0.249}$	0.983	0.96
Living branches excl. needles	$3.992*d^{3.285}*l_{cl}^{-0.804}$	0.960	3.06
Needles	$33.203*d^{2.132}*l_{cl}^{-0.502}$	0.971	1.13
Dead branches	$3101.458*d^{0.307}*h_{rel}^{5.275}$	0.823	2.85
Norway spruce			
Stem over bark	$38.711*d^{1.789}*h^{0.901}$	0.999	0.25
Silver and downy birch			
Stem wood	$6.329*d^{1.820}*h^{1.580}$	0.999	0.47
Stem bark	$5.156*d^{1.197}*h^{1.456}$	0.981	0.29
Living branches excl. leaves	$3.775*d^{2.966}*h_{rel}^{-0.745}$	0.960	0.67
Leaves	$13.180*d^{1.978}$	0.983	0.12
Dead branches	$1130.121*d^{1.693}*h^{-2.146}$	0.900	0.16

Appendix 9. Tree height, crown length, stem wood volume and stem wood density of pines, spruces and birches in different diameter classes on mineral soils. The variables were obtained from the NFI data. Stem wood density was determined as the relation between the biomass estimated using Marklund's (1988) models and stem wood volume estimated by Laasasenaho's (1982) functions, and by Hakkila's (1979) models.

Appendix 10. The differences in tree height, crown length, stem wood volume and stem wood density between fertile and infertile mineral soils. If the difference is positive, the trees growing on fertile mineral soils have larger values for these characteristics. If the difference is negative, the trees growing on infertile mineral soils have larger values.
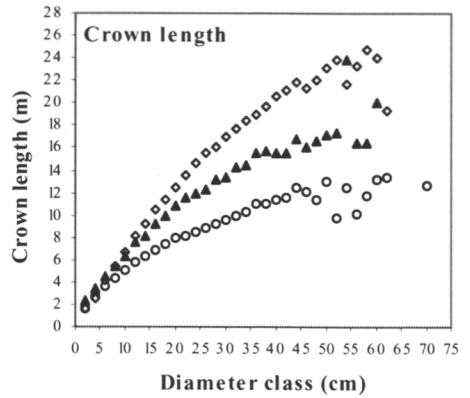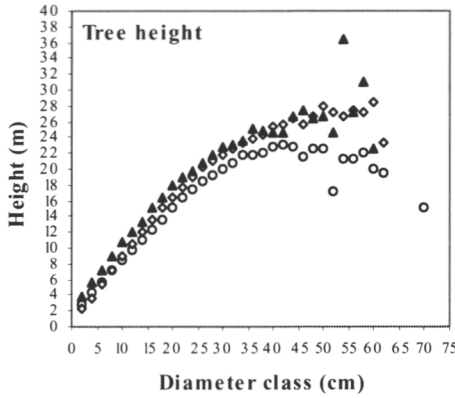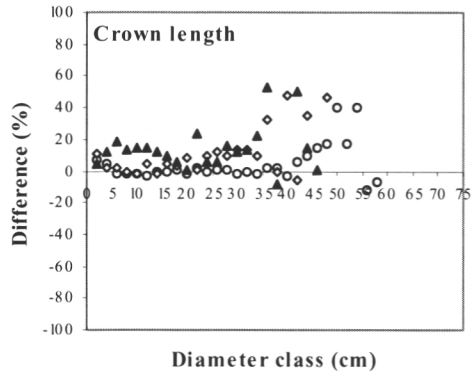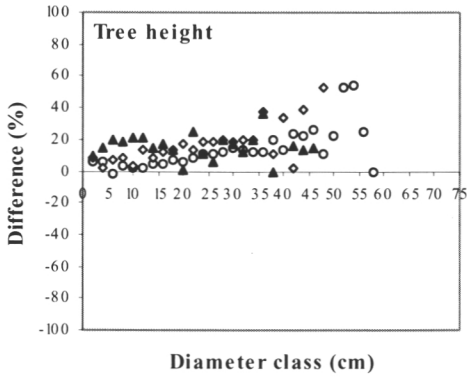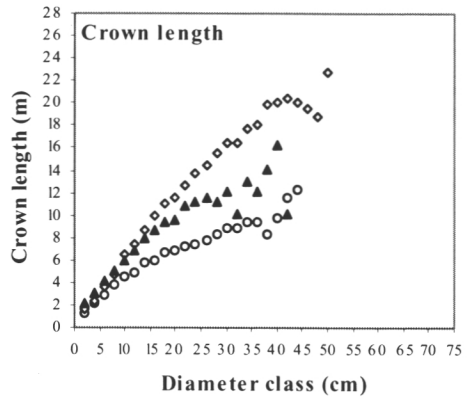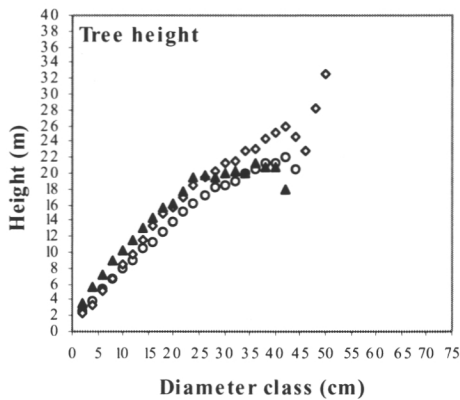

○ pine ◇ spruce ▲ birches
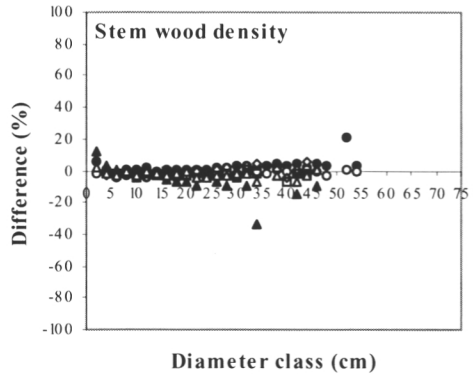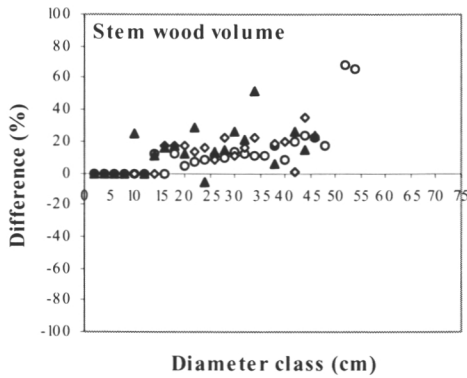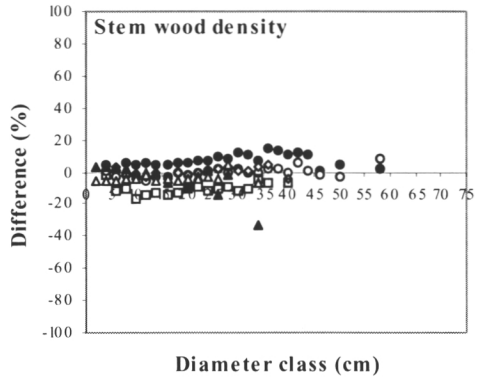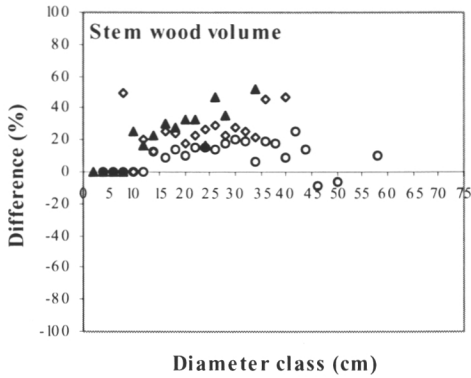
○ pine ◇ spruce ▲ birches

● Marklund (pine)   ○ Hakkila (pine)

◇ Marklund (spruce)   □ Hakkila (spruce)

▲ Marklund (birches)   ▵ Hakkila (birches)

Appendix 11. The biomass of above-ground components of trees and the differences in the biomass of above-ground components of pines between fertile and infertile mineral soils and between Southern and Northern Finland. In the left figure, the biomass of above-ground components of trees was estimated for trees in the NFI data using coefficients obtained from Kauppi et al. (1995), and mean basic densities of stems obtained from Hakkila (1966). The volumes in the NFI data were estimated using Laasasenaho's (1982) functions. In the right-hand figure, the differences were estimated using Korhonen and Maltamo's (1990) biomass model for above-ground components of pine. If the difference is positive, the trees growing on fertile mineral soils or in Southern Finland have larger values. If the difference is negative, the trees growing on infertile mineral soils or in Northern Finland have larger values.

o pine   ◇ spruce   ▲ birches

o pine (site fertility)   ● pine (location)

Appendix 12. The differences in tree height, crown length, stem wood volume and stem wood density between Southern and Northern Finland on mineral soils. If the difference is positive, the trees growing in Southern Finland have larger values. If the difference is negative, the trees growing in Northern Finland have larger values.
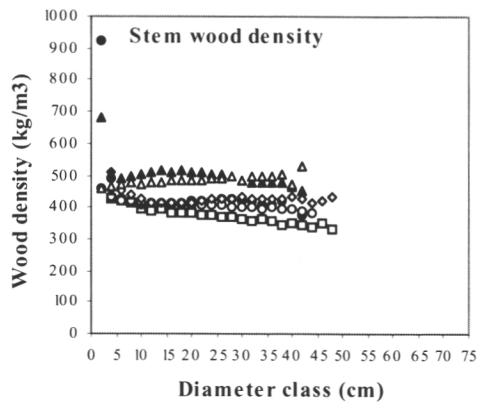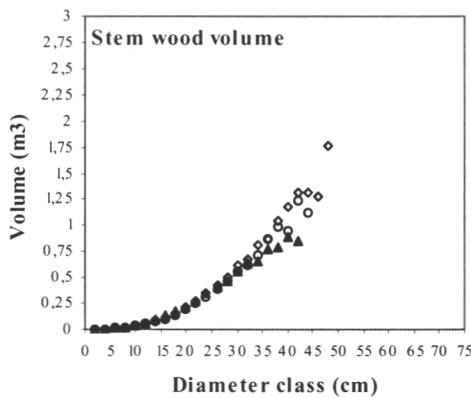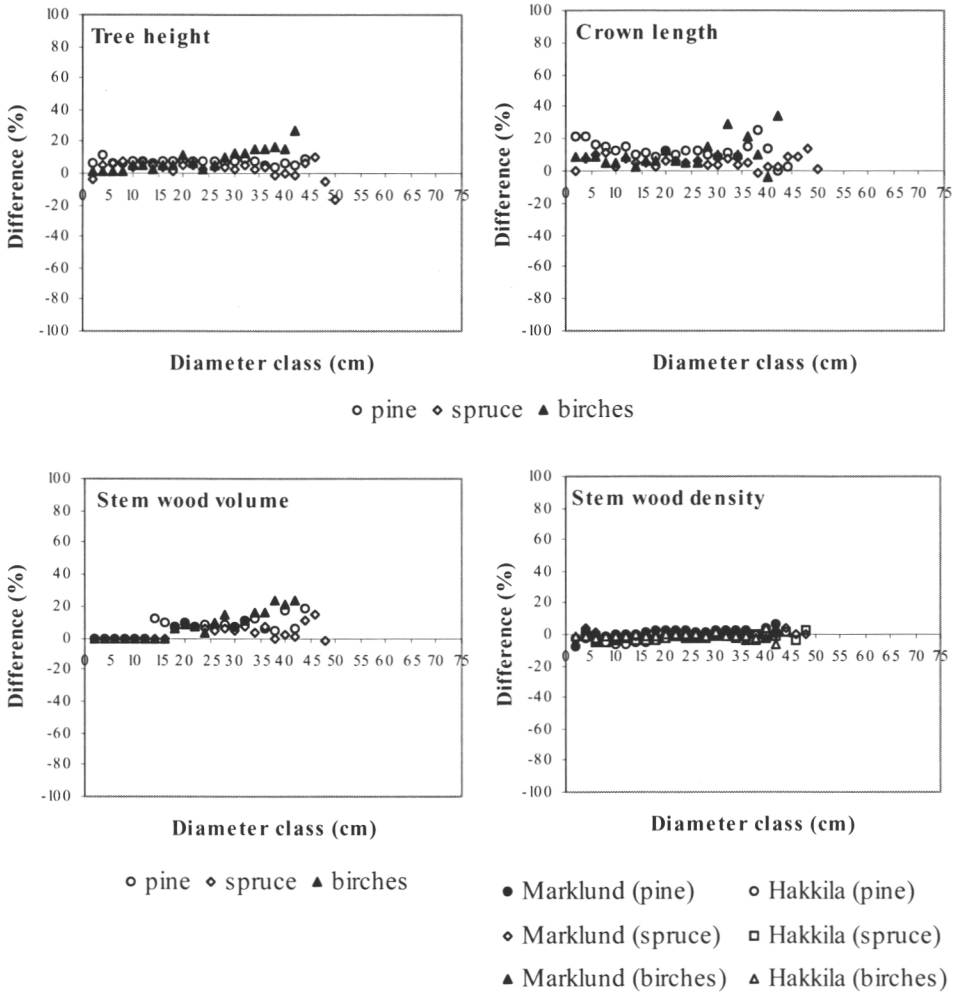

o pine   ◇ spruce   ▲ birches

o pine   ◇ spruce   ▲ birches

● Marklund (pine)   o Hakkila (pine)

◇ Marklund (spruce)   □ Hakkila (spruce)

▲ Marklund (birches)   ▲ Hakkila (birches)

Appendix 13. Tree height, crown length, stem wood volume and stem wood density of pines, spruces and birches in different diameter classes on peatlands. The variables were obtained from the NFI data. Stem wood density is determined as the relation between the biomass estimated using Marklund's (1988) models and stem wood volume estimated by Laasasenaho's (1982) functions, and by Hakkila's (1979) models.
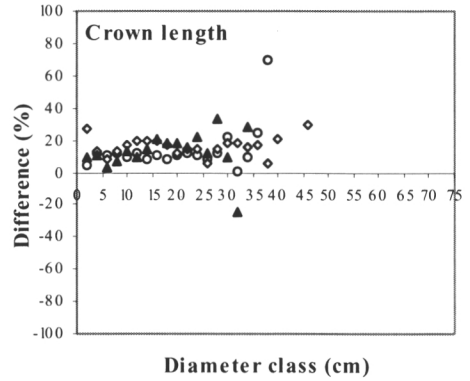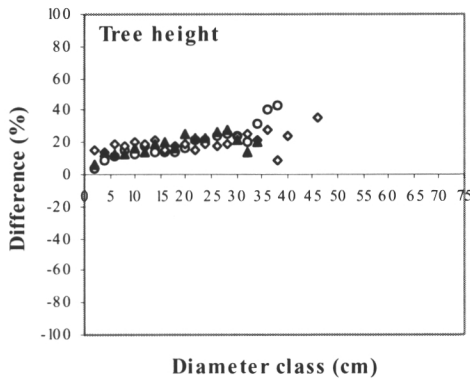

o pine ◇ spruce ▲ birches

o pine ◇ spruce ▲ birches

● Marklund (pine)   o Hakkila (pine)

◇ Marklund (spruce)   □ Hakkila (spruce)

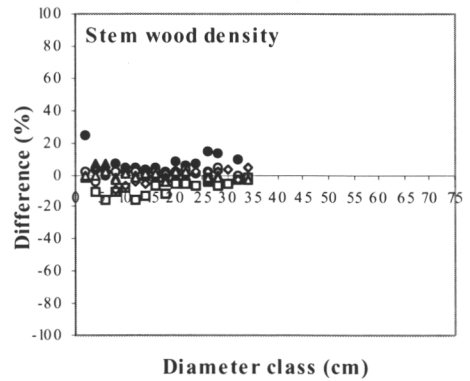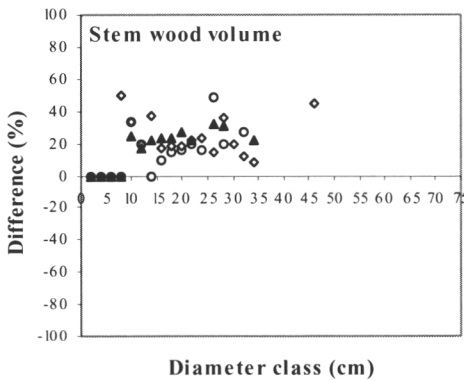▲ Marklund (birches)   ▵ Hakkila (birches)

Appendix 14. The differences in tree height, crown length, stem wood volume, stem wood density between mineral soils and peatlands. If the difference is positive, the trees growing on mineral soils have larger values. If the difference is negative, the trees growing on peatlands have larger values.

Appendix 15. The differences in tree height, crown length, stem wood volume, stem wood density between peatlands in Southern Finland and peatlands in Northern Finland. If the difference is positive, the trees growing in Southern Finland have larger values. If the difference is negative, the trees growing in Northern Finland have larger values.
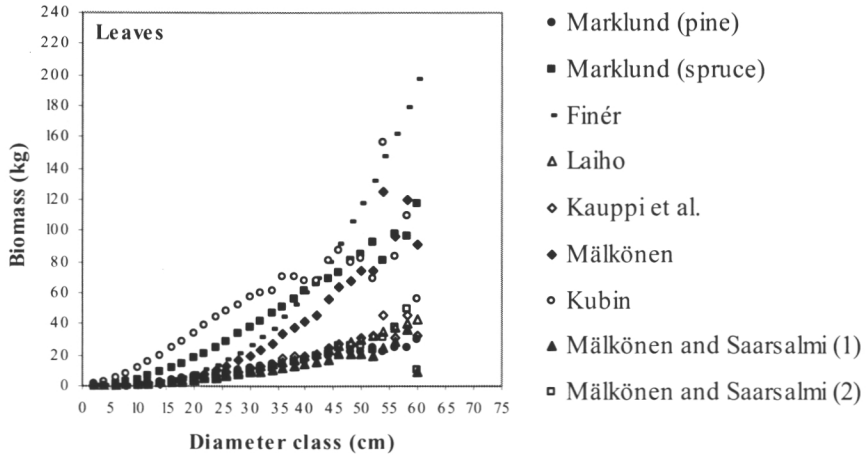

o pine   ◇ spruce   ▲ birches

o pine   ◇ spruce   ▲ birches

● Marklund (pine)   o Hakkila (pine)

◇ Marklund (spruce)   □ Hakkila (spruce)

▲ Marklund (birches)   ▲ Hakkila (birches)

Appendix 16. The biomass of birch leaves in the NFI data estimated by Marklund's (1988) models for pine and spruce, Mälkönen's (1977), Kubin's (1982), Mälkönen's and Saarsalmi's (1982), Finér's (1989), Kauppi's et al. (1995) and Laiho's (1997) models.