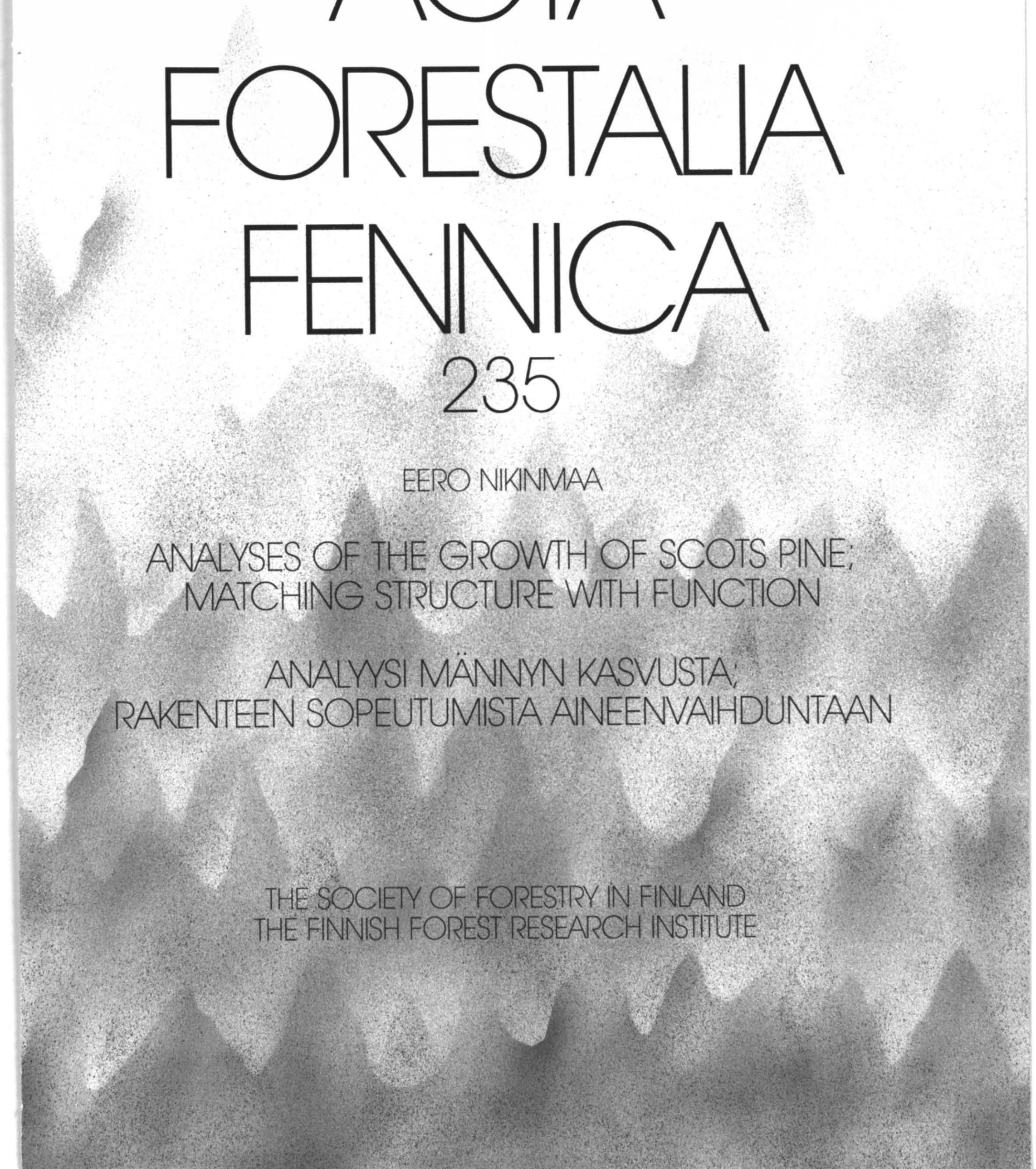

ACTA FORESTALIA FENNICA

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EERO NIKINMAA

ANALYSES OF THE GROWTH OF SCOTS PINE; MATCHING STRUCTURE WITH FUNCTION

ANALYYSI MÄNNYN KASVUSTA; RAKENTEEN SOPEUTUMISTA AINEENVAIHDUNTAAN

THE SOCIETY OF FORESTRY IN FINLAND
THE FINNISH FOREST RESEARCH INSTITUTE

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ANALYSES OF THE GROWTH OF SCOTS PINE; MATCHING STRUCTURE WITH FUNCTION

Analyysi männyn kasvusta; rakenteen sopeutumista aineenvaihduntaan

Eero Nikinmaa

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium XII of the University Main Building, Fabianinkatu 33, on 26 March 1993, at 12 o'clock noon.

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A theoretical framework to analyse the growth of Scots pine (*Pinus sylvestris* L.) is presented. Material exchange processes and internal processes that transport, transform and consume materials are identified as the components of growth. Hierarchical system is lined out. Momentary uptake of material at a singe exchange site depends on the environmental condition next to the exchange site, the internal state of the biochemical system of the plant and the structure of the plant. The internal state depends on the exchange flows over a period of time and the structural growth depends on the internal state. The response of these processes to the fluxes is controlled by the genetic composition of the plant.

The theoretical framework is formulated into a mathematical model. A concept of balanced internal state was applied to describe the poorly known internal processes. Internal substrate concentrations were assumed to remain constant but tissue-specific. A linear relationship between the quantity of foliage and wood cross-sectional area was assumed to describe balanced formation of structure. The exchange processes were thus described as a function of external conditions. The stand level interactions were derived from shading and effects of root density on nutrient uptake.

The approach was tested at different levels of hierarchy. Field measurements indicated that the hypothesis of the linear relationship described well the regularities between foliage and sapwood of a tree within a stand when measured at functionally corresponding height. There was considerable variation in the observed regularities in the range of geographic occurence of Scots pine. Model simulations gave a realistic description of stand development in South Finland. The same model was also able to describe the growth differences in Lapland after considering the effect of growing season length in the parameter values. Simulations to South Russia indicated stronger deviation from the observed patterns.

The simulations suggested interesting features of stand development. They indicated strong variability in the distribution of carbohydrates between tree parts during stand development. Internal circulation of nutrients and the reuse of the same transport structure by various needle generations had a strong influence on the simulation results. Similarly, the extension growth of shoots and their forking was identified as an important process from the point of view of the growth of whole tree.

Tämä työ esittelee teoreettisen viitekehyksen männyn (*Pinus sylvestris* L.) kasvusta puun elintoimintojen osana. Elintoiminnot jaetaan aineen vaihtamiseen kasvin ja ympäristön välillä ja kasvin sisäisiin reaktioihin. Jälkimmäisiin lasketaan aineiden kuljetus, niiden muutokset eri yhdisteiksi ja niiden kulutus kasvuun. Elintoiminnot muodostavat hierarkisen systeemin. Kasvin sisäinen tila, rakenne ja lähiympäristö määräävät vaihtoreaktioiden nopeudet hetkellisesti. Sisäinen tila muuttuu vaihtoreaktioiden tuloksena hitaasti ja rakenne kasvaa asteittain muuttuvan sisäisen tilan perusteella. Edellä mainittujen reaktioiden vasteet systeemissä tapahtuviin virtauksiin määräytyvät geneettisen säädön tuloksena.

Teoreettisen viitekehyksen pohjalta laadittiin matemaattinen malli, jonka avulla lähestymistapaa arvioitiin. Huonosti tunnettujen sisäisten reaktioiden vaikutus kasvuun saattiin olettamalla, että kasvin sisäinen tila pysyy jatkuvasti tasapainossa. Puun eri osien ravinnepitoisuudet oletettiin ajan suhteen vakioiksi ja neulasten ja vettä johtavan puuaineen poikkileikkausalan välillä oletettiin lineaarinen riippuvuus. Vaihtoreaktioiden nopeudet riippuivat pelkästään ulkopuolisista olosuhteista vakion sisäisen tilan olettamuksesta johtuen. Metsikkötason vuorovaikutukset seurasivat varjostuksesta ja juuristokilpailun vaikutuksesta ravinteiden ottoon.

Lähestymistapaa testattiin kahdella tavalla. Hypoteesi, että lineaarinen riippuvuus kuvaa neulasten ja puuaineen välistä suhdetta, sai tukea samoissa ilmasto-olosuhteissa tehdyissä mittauksissa, kun puuaineen poikkileikkauspinta-ala mitattiin fysiologisesti vastaavalta korkeudelta eri puissa. Eri ilmasto-olosuhteissa riippuvuuden kulmakerroin oli selvästi erilainen. Simulointitulokset vastasivat Etelä-Suomen metsiköiden kasvun kehityssarjoja. Toisaalta Lapin ja Etelä-Suomen metsien kasvuerot seurasivat kun kasvukauden pituus muutettiin vastaamaan Pohjois-Suomen olosuhteita. Vastaava yritys Etelä-Venäjän metsiin ei antanut yhtä hyviä tuloksia.

Simulointitulokset osoittivat mielenkiintoisia piirteitä metsikön kasvuun vaikuttavista seikoista.Tulosten valossa näyttää selvältä, että metsikön kehityksen kuluessa hiilihydraattien jakautuminen puun eri osien välillä muuttuu selvästi. Myös ravinteiden sisäisellä kierrolla ja tavalla, millä usean sukupolven neulaset hyödyntivät saman puuaineen kuljetuskapasiteetin, oli ratkaiseva merkitys metsikön simuloituun kehitykseen. Edellisten lisäksi versojen pituuskasvu- ja haaroittumistavalla oli selvä vaikutus metsikön kehitykseen.

Keywords: growth models, partitioning of growth, carbon budget, nutrients, structure, pipe model, heartwood, growth, Scots pine.
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Contents

List of main symbols

Variable	**Unit**	**Explanation**
Y_i	kg/ha	Stand level biomass of plant compartment i, i=tot,n,b,st,tr,f
N		Number of trees
W_i	kg	Dry weight of plant compartment i , i=tot,n,b,st,tr,f
Gi	kg	Growth of plant compartment i, i=n,b,st,tr,f
S_i	kg	Senescence of plant compartment i, i=n,b,st,tr,f
I	kg	Annual resource inflow
O	kg	Annual resource outflow
α_i		Allocation coefficient of plant compartment i, i=n,b,st,tr,f
ω_{Ci}	kg dm/ kg C	Conversion efficiency of carbon to structure in plant compartment i, i=n,b,st,tr,f
ω_{Ni}	kg dm/ kg N	Conversion efficiency of nutrient to structure in plant compartment i, i=n,b,st,tr,f
ι		Degree of interaction
z	m	Specific height in the canopy
P(k)	kg C	Annual photosynthetic production by a tree at year k
P_0	kg C/kg dm	Annual photosynthetic production at unshaded conditions per unit area of needles
h_{max}	m	Maximum height of the canopy
h_{min}	m	Minimum height of the canopy
χ	m^2/m	Needlearea density at height z
R(k)	kg C	Annual maintenance respiration of a tree at year k
r_{mi}	kg C/ kg dm	Mass specific annual respiration rate for plant compartment i, i=n,b,st,tr,f
$r^*{}_{mi}$	kg C/kg dm/h	Respiration rate at chosen base temperature for plant compartment i, i=n,b,st,tr,f
E	h	Extend of the active period
$\overline{T}$	°C	Average temperature of the active period
T_b	°C	Base temperature of the respiration rate
e_{f_*}	kg N/kg dm	Fineroot mass specific annual nutrient uptake
e_f^*	kg N/kg dm	Fineroot mass specific annual nutrient uptake without competition
D_f	kg /ha	Threshold density of roots in soil
U	kg	Annual nutrient uptake
T	kg	Annual retranslocation of nutrients
ξ	kg N/kg dm	Amount of the nutrients retranslocated from senescing needles
π_i	kg N/kg dm	Nutrient concentration of the plant compartment i, i=n,b,st,tr,f
ε_i	m^2/kg	Wood cross-sectional area per needle mass per length of plant compartment i, i= b,st,tr,sh,w
γ_i	kg/m^3	Bulk density of wood of plant compartment i, i=b,st,tr,sh,w
l_i	m	Length of woody structure of plant compartment i, i=b,st,tr,sh,w
H_i	kg	Turnover of sapwood into heartwood in plant compartment i, i=b,st,tr
η		Ratio between shoot length and diameter
ν		Number of mother shoots in the unit of calculation
h_t	m	Total tree height
h_{cb}	m	Height of the crown base of tree
ϕ	m^2/kg	Specific needle area
λ		Lagrange multiplier
σ_{na}		Proportion of annual senescence of needles in age class a
σ_f and σ_{tr}		Proportion of annual senescence of fine roots and transport roots
σ_b		Proportion of annual foliage senescence associated with heartwood formation in branches
m_r		Tree mortality rate parameter
m_t		Tree mortality threshold parameter
τ		Decrease in the number of stems for other reasons
κ		Production of new photosynthesis per invested photosynthetic products
d_i	m	Diameter of plant compartment i, i=b,st
h_{med}	m	Average height of trees
A	a	Age of trees
A_b	a	Age of branches

The following subscripts and superscripts are used:

j	stands for size classes
i	stands for plant compartments
q	stands for branch
k	stands for specific year
a	stands for age class

tot = total mass (all biomass compartments together)
n = needles
b = branches
st = stems
tr = transport roots
f = fine roots
s = structure associated with senescing needles

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1 Introduction

1.1 Process-based tree and stand growth models

The traditional methods of modelling the growth of trees and stands describe the growth of certain dimensions of trees or stands with time-dependent functions that are based on observations of the past growth of the same dimensions in similar conditions (e.g. Nyyssönen and Mielikäinen 1978). Presently the environment and treatment regimes of forests are changing. Also, forestry is practised in areas where there is no tradition of forest management. These changes imply situations in which the history of the growth of the present stands is not know or in which it is different from what can be expected in the future. The bases of the traditional methods of growth modelling become thus less valid. This is especially so if the differences in the growth conditions between the past and the present affect the dynamic processes driving growth (Bossel 1991). For these reasons, more careful analyses of the underlying mechanisms that produce growth become important in the growth and yield studies.

Growth of plants is accumulation of matter into organisms. Material balances are quite a natural starting point for the analyses of growth and yield. The state variable approach developed for systems analysis is a tool for such analyses (e.g. Thornley 1981; de Wit and Penning de Vries 1983). A system that is studied is described with a set of state variables. They are connected to each other through flows of material. The states of the state variables determine the rate of these flows. At an aggregate level, the change of state of a tree can be seen as the difference between the in- and out-flows of material in tree-environment system.

The selection of state variables is one of the key approximations and assumptions of a model (Thornley 1981). Ecological systems are hierarchical, i.e. phenomena occur at different spatial and temporal scales (e.g. Levin 1988). The observed patterns depend both on the system properties and on the scale at which they are studied (Levin 1988). According to de Wit (1982), the system studied should be limited so that a minimum interaction should take place between the environmental driving variables and the system state variables. However, this limitation depends on the purposes of the analyses and the hierarchy level at which the system is studied.

The state variable approach suffers from a difficulty in describing the mechanisms that form the internal communication system of plants, in addition to the problems associated with the correct limitation of the system (de Wit and Penning de Vries 1983). Especially the distribution of resources between tree parts is problematic to model on mechanistic basis (Nikinmaa 1992).

An approach to study these kinds of phenomena associated with tree growth is to assume a goal for the system or for some level of the system based either on observation or arguments that can be justified, e.g., by evolutionary arguments (Thornley and Johnson 1990). Models can then be used to study the consequences of such assumption on other aspects of the studied phenomena and also to establish some limits for the system behaviour under the assumed conditions (Thornley and Johnson 1990; Sharpe and Rykiel 1991; Givnish 1985). This approach has been used to model the distribution of growth in material balance models (e.g. Davidson 1969; Reynolds and Thornley 1982; Mäkelä 1986; Valentine 1985; Hari et al. 1990; Ludlow et al. 1990).

The so called functional balance (Brouwer 1962) and pipe model theory (Shinozaki et al. 1964) are examples of growth-guiding principles in process-based stand growth models. The concept of functional balance was developed based on the experimental observations that the carbohydrates were distributed between the shoot and root growth so that the internal nutrient concentration remained stable (Brouwer 1962). On the other hand, the regular ratios between dimensions of different parts of trees have been used as a goal for distribution of growth between foliage and wood or different compartments of wood in carbon budget based models (e.g. Hari et al. 1985; Mäkelä 1986; Valentine 1985; Landsberg 1986; Ludlow et al. 1990; Sievänen 1992).

1.2 The objectives

The process-based tree and stand growth models offer a valuable tool for analyses of tree growth in the present rapidly changing environment. The models based on biological mechanisms, however, suffer from insufficient knowledge on some of the central processes and also from being rather complicated. An approach that uses some, either empirically or theoretically justifiable principle to describe badly known functions can offer a simpler alternative for the process-based analyses of the stand development.

The objectives of this work are a) to develop theoretical bases to analyse Scots pine (*Pinus sylvestris* L.) growth within the material budget framework, b) to evaluate if the assumption of balanced internal state as a principle for growth can be applied within this framework and c) to study the patterns of growth of trees and stands caused by the stand development from above premises. The work is divided into three components. First the theoretical framework used to analyse the functioning of tree is outlined. The main emphasis is paid on clarifying the roles of structure, function and growth. Second, a model of tree and stand growth is designed assuming that growth is the means of trees to balance structure with function. The key assumptions are defined exactly and a set of additional assumptions is introduced to make the model operational. Third, the approach is analysed by a) testing the generality of the hypothesis that a balanced internal state is expressed in a constant ratio between the amount of foliage and the sapwood cross-sectional area below and b) comparing various aspects of simulated growth against observed patterns. Furthermore, the general implications of the used assumptions on growth are studied and the applicability of the approach is discussed.

2 Analysis of stand development

2.1 Connection between functions, structure and environment

2.1.1 Spatial and temporal hierarchy in forests

The growth and development of a forest stand can be analysed within a framework of material flows and various processes operating at different spatial and temporal scales. The outcome of these is the formation of organic structures (e.g. Pomeroy et al. 1988). The basic theoretical framework for tree growth can be presented as in Figure 1. Momentary exchange of material between plants and the environment takes place at various exchange sites. Internal processes mix the materials taken up and transform them into different organic compounds and to permanent structures of the plants. The rates of exchange processes are determined by the local environment and the local internal state of each exchange site. The internal state consist of the concentrations of different substrates and organic compounds. It changes more slowly since it results from the action of various exchange sites. The permanent structure is the "skeleton" in which the various processes take place. It changes even more slowly, since it responds to the changes in the internal state. However, the structure affects both the local environment of the exchange sites and the internal processes of the plant. Thus there is a feedback loop from the accumulated growth of many years to these rather fast reactions. The success of the whole in the past determines what kind of momentary reactions are possible at the moment.

The environmental conditions of site, i.e. climate, concentration of gases in the air, physical and chemical soil properties, i.e. the distribution of particle sizes, their structure and chemical composition, determine the magnitude of the flows within the system. The climatic phenomena and the concentrations in the air are largely independent of the local stand level processes due to effective mixing of substances in the atmosphere. In contrast, the light climate and the soil properties do not remain stable. Vegetation changes them within the time scale of growing season and rotation. The soil properties also change slowly, within a time range of hundreds and thousands of years (e.g. Ulrich 1987). The environmental conditions thus have a similar temporal and spatial hierarchy as the plant's response to the environment. At any given moment, the past and present environmental condition determine the functions of the outlined system.

2.1.2 Components of tree growth

2.1.2.1 General overview

Tree growth can be interpreted as acclimation to the environmental conditions that have prevailed in the growing site. The rather slow growth processes use the materials from the fast exchange processes within the limits of the genetic information that remains stable for each individual. The net growth of a plant can thus be divided into the components of material in- and outflows and into the growth and senescence processes.

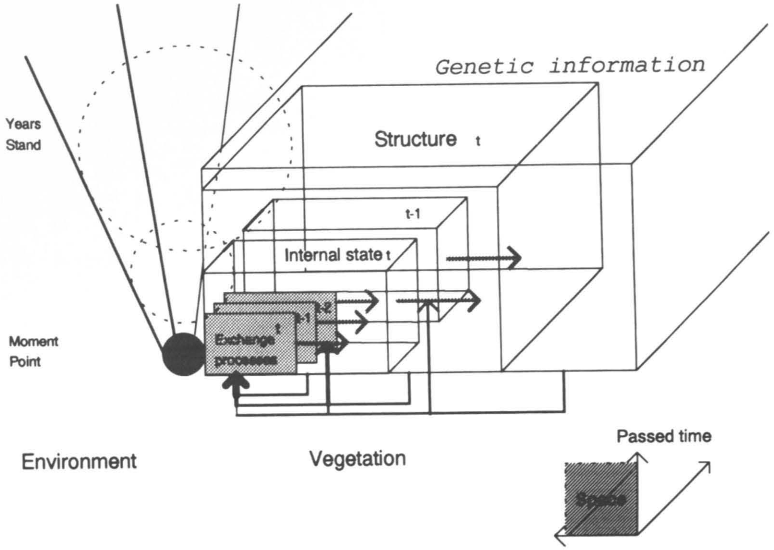

Figure 1. A schematic presentation of the spatial and temporal hierarchy in the functions of a forest. The exchange processes describe the flows in and out of the plant, the internal state means the internal consentration of substrates and readily reversible chemical compounds within the plant. In the internal processes materials taken up are transported between different parts of a plant and transformed into active and storage compounds and into structure. The structure means the permanent "skeleton" of the plant in which the exchange and internal processes take place.

The most important material flows are those of carbon, water and nutrients. In the following, the way by which stand level effects determine the immediate environment at the exchange site is reviewed. This is followed by a treatment of the momentary processes at the exchange sites and how the use of materials taken up and the flows of other substances affect them. A separate review is given on the effects of temperature on both the exchange and the internal processes followed by a review on the control of growth and senescence processes. Finally, a review on the functional properties of the structure is required to get a full picture of the role of growth in the tree functions, since the structure affects functions also through providing an infrastructure for different processes.

2.1.2.2 Stand level interactions and material flows reaching exchange surfaces

Interferences between individuals within a stand and the size of an individual determine the proportion that the individual captures from the total flux reaching the site. The amount of materials reaching the exchange surfaces depends on the spatial distribution of the exchange sites. The closer the sites are the more they interact with each other. Thus the interaction between sites is highest within an individual. From the whole plant point of view this is unimportant since the resources captured are used by the same organism. However, different spatial arrangements of the exchange sites can affect the amount of resources used to bring about the uptake (e.g. see chapter 2.2.4, Givnish 1985; Küppers 1989).

The interplant interference depends on the number of exchange sites of different individuals that can intercept the same flux. Also the position of these sites relative to each other is important, if there is a clear direction of the flux, as it is the case with light. The probability that an exchange site can intercept certain flux is often described with a negative exponential function of the total amount of exchanging or intercepting sites at stand level (e.g. Monsi and Saeki 1953; Fitter 1987). In order to describe the interaction between trees of a stand an assumption of horizontal homogeneity is often used (e.g. Kellomäki et al. 1980). However, the approach can be adapted to consider the spatial distribution of foliage more precisely (e.g. Mohren 1987; Mäkelä 1990a) or the stands can be considered to consist of individual trees with certain crown form distributed into the space in known fashion (Kuuluvainen and Pukkala 1987, 1989; Grace et al. 1987a,b; Oker-Blom et al. 1989). According to Donald (1963) competition begins when the immediate supply of a single necessary factor for plants falls below the combined demands of the different exchange sites of the plants.

2.1.2.3 Material fluxes

The velocities of material flows are different in atmospheric and soil environment. It seems that the actual speed of transport processes in soil may influence the acquisition of nutrients more that the capacity of roots to absorb ions (Clarckson and Hanson 1980). In the atmosphere, on the other hand, the effective mixing of air guarantees the speed of transport processes to the proximity of leaves so that it rarely affects the inflow.

The flow of carbon into the plant at the exchange surface depends on the rate at which carbon is transformed to sugars in cells and the conductivity of the transport path from the surface of the leaf to the chloroplasts. The transformation rates depend on the availability of light and the internal state of the photosynthetic "machinery". The photosynthetic rate depends on the light supply in saturating fashion (e.g. Hari et al. 1988). This indicates that the rate is initially limited by light supply but at high light intensities either by carbon supply or other factors. For example, the chlorophyll density within leaves affects the shape of the light response curve (Leverenz 1987).

The uptake by roots at the exchange site depends on the number of ion carriers in the cell membranes and their activity (Clarkson 1985). There is also some evidence of allosteric regulation of nutrient uptake (e.g. Jensen and Pettersson 1978; Clarkson 1985). However, roots acclimate to changing conditions most likely through changes in number and type of ion carriers (Clarkson 1985).

The substances taken up are assimilated into organic compounds and used for growth of the plant. The transformation of the materials taken up into other compounds can have strong influence on the rates of inflow when the quantities of inflow over a period of time are considered instead of the momentary rates of inflow (see Figure 1, feedback arrow from internal processes to the exchange processes). There seems to be a close connection between the growth rate and the uptake rate of especially nitrogen (Ingestad 1979; Ingestad 1981; Clarkson and Hansen 1980). The regulation of nutrient uptake and consumption seem to cause that the actual steady-state concentrations of nutrients in roots are quite independent of external ion concentrations (see review by Clarkson 1985). On the other hand, the effects of the sink-source relationships of carbon on its uptake rates are still unclear (Geiger and Servaites 1991). They suggest that the actual changes in the uptake rates may be connected to a non-specific signal associated with the changes in source-sink relationship.

The uptake of one substance can depend on the simultaneous exchange of other substances, since the flows of several substances occur through the same exchange sites (see Figure 1, feedback arrow from internal processes to the exchange processes). For example, there is an obvious trade-off between the loss of water and gain of carbon in terrestrial plants. The stomatal regulation controls simultaneously both carbon inflow and water outflow, but the mechanisms of this regulation are not yet fully understood. Models based on control theory and optimisation (e.g. Cowan and Farquhar 1977; Hari et al. 1986; Hari and Berninger 1990) have been quite successful in predicting the photosynthetic production in natural conditions (e.g. Hari and Berninger 1990; Berninger and Hari, in press). Overall, it seems that the stomatal conductance depends on the water availability, temperature, light, and water and carbon dioxide concentrations in the air near the leaf since these together determine the concentration gradients of carbon dioxide and water vapour between leaf and the surrounding air (e.g. Jarvis et al. 1981).

The flows of water and nutrients are in the same direction so they should have synergetic effects. The convection of water is able to supply enough of certain nutrients in fertilised agricultural soils (Clarkson and Hansen 1980) but it seems that plants are able to maintain sufficient nutrient uptake independent on water flow (Boyer 1985). Nitrate uptake seems to be proportional to the flow of water only at very low water fluxes. This could be attributed to an inhibition of uptake caused by an accumulation of nitrate ions in the roots (Boyer 1985). According to Boyer (1985), on the other hand, in conditions of low water uptake nutrient uptake can create positive xylem pressure in roots by creating osmotic potential difference between soil and root, thus enhancing water uptake. Thus the uptake of nutrients seems to be independent of water flow. However, in conditions of low water availability, the transport of nutrients in soil to the vicinity of roots can strongly limit the uptake (e.g. Nye and Tinker 1977; Chapin 1991)

The rate of flow through exchange sites depends also on the fluxes at other parts of the plant (see Figure 1, exchange processes creating the internal state and feedback arrow from internal processes to the exchange processes). Especially the in- and out-flows of water are closely coupled. The driving force and the conductance of the flow path affect the water movement (Boyer 1985). The reactions that affect transpiration are quite important for water uptake. There is growing evidence that roots can directly affect the stomata through interactions between the content of nutrients and the abscisid acid in the sap (e.g. Boyer 1985; Schultze 1991; Tardieu et al. 1992a,b). Schultze (1991) has also suggested that the quite constant relationship between the water potentials of leaf and root xylem might be associated with phloem transport and the osmotic pressure difference of phloem between shoots and roots. This could provide trees with a fast signal from roots to shoot as a response of soil drying.

The internal processes require energy, which releases carbon from the system. The respiration processes can be divided according to the processes in which the energy is used (e.g. Penning de Vries et al. 1974). Growth, maintenance and transport respiration can be identified. Maintenance can also be interpreted as resynthesis of degraded dry mass that does not require uptake of new material but requires input of energy (Thornley and Johnsson 1990).

The release of carbon dioxide from the biosynthesis can be calculated based on the chemical reactions involved (Penning de Vries 1975). These calculations can be extended to the whole plant level if the chemical compositions of different plant compartments are known (e.g. Mohren 1987). However, as shown by Chapin et al. (1987), quite considerable changes in the total energy requirement can exist depending on the chemical pathway used to build up compounds, especially proteins from different forms of nitrogen taken up by the plant.

Maintenance respiration results from the resynthesis of substances, mainly proteins, and of the maintenance of ion gradients (de Wit et al. 1978 and Penning de Vries and van Laar 1982; cited by Mohren 1987). Although maintenance respiration can be estimated based on the concentration of proteins and the metabolic activity of the tissue (e.g. Mohren 1987), there is large variability in the reported values (e.g. Schäfer et al. 1991). Especially the metabolic activity of tissues varies according to, e.g., the age of the tissue and the environment (Mohren 1987; Pell and Dann 1991).

An increased availability of one resource can affect the uptake of another by changing the biochemical machinery of the uptake organ (see Figure 1, feedback arrow from internal processes to the exchange processes). Evans and Terashima (1987) and Evans (1987) reported that nitrogen availability and acclimation to high irradiance conditions had an effect on the relative activities of light and dark reactions of photosynthesis. The acclimation to high nitrogen availability favoured dark reactions and the acclimation to high light intensity light reactions. Also the nutrient availability, especially that of phosphorus, affects the permeability of roots to water (Passioura 1988). In addition, plants seem to be able to improve soil conditions for nutrient uptake in their vicinity and create favourable conditions to micro-organisms around the root surfaces by excreting energy rich compounds (see review by Clarckson and Hansen 1980; Clarkson 1985).

There are numerous substances that can be either quite neutral from the plants point of view or can have toxic effects on plants. For example, such a common substance in soil as aluminium may have strong influence on the functions of a plant, especially if the soil environment is changing through human activities (Ilvesniemi 1991).

2.1.2.4 Effects of temperature

Temperature has a strong influence on the process rates. The input/output processes, especially those of water, can to some degree influence the energy balance of plants and thus the internal temperature of a plant, but mostly the ambient temperature determines it.

Temperature effects have different time scales. Temperature affects the rates of processes directly, and indirectly by creating periodic unfavourable conditions for plants inducing dormancy. Generally an increase in temperature causes an exponential increase in process rates. At normally occurring temperature range a 10 degree rise in temperature doubles the process rate (Landsberg 1986). This model explains quite well the measured respiration rates although there seems to be quite big variation during the growing season (e.g. Landsberg 1986). The acclimation or adaptation of plant to cold climate changes the temperature dependence of respiration and also photosynthesis (see review by Skre 1991). Cold adapted plants have a higher dark respiration rate at a given temperature than warm adapted ones and their optimum temperature for the exchange rate of carbon dioxide is lower. The latter effect seems to be connected with enzyme activities resulting in high mesophyll conductance at low temperatures. In addition, the high rates of photorespiration at high temperatures may play a role in these plants (Skre 1991). Temperature has also been reported to affect the light saturation of photosynthesis (e.g. Sprugel 1989).

In boreal and temporal climatic zones trees that become active too early in the spring or those that continue the active phase too long in the autumn have the risk of serious damage. In the opposite case quite strong losses of growth can occur. The adaptation to cyclic environment is a typical example of feedback from the genetic level to the internal processes. The annual cycle is seen in various aspects of functions of trees such as the timing of growth and dormancy periods in apical meristems (e.g. Sarvas 1972, 1974), the frost hardiness of trees (e.g. Repo et al. 1991), the rates of input output processes (e.g. Pelkonen and Hari 1980; Pelkonen 1981). The induction, maintenance and release of dormancy are triggered by environmental factors, including 1) temperature, 2) photoperiod, 3) water stress and to lesser extent 4) mineral deficiency and 5) light quality (Lavender and Silim 1987). It also seems that the stage of development of a tree (seedling vs. mature), genetic variation within species and the species properties affect the dormancy set and release (e.g. Kozlowski 1971a; Koski and Sievänen 1985; Hänninen 1990).

The accumulated temperature during the growing period and the day length seem to be connected with the induction of rest period (e.g. Koski and Sievänen 1985). On the other hand, dormancy release is largely determined by temperature; first a period of cold temperatures (between –5 and 10 °C) is required to remove the growth arresting physiological conditions in buds and then certain amount of accumulated forcing temperature (> 0 °C) is required for bud burst (cf. Hänninen 1990).

2.1.2.5 Growth

The rates of the various input processes determine the availability of materials for growth but also the rates of the internal processes bringing about growth influence the rate of uptake processes (see Figure 1). The internal regulation of these processes at the whole plant level is still quite poorly known, partly because of the difficulties involved in this kind of analysis (Lavender and Silim 1987; Schulze 1991). As argued in Chapter 2.1.1, the whole growth history of the plant species can be involved in the regulation of growth through the limits set by the genetic information (see also Figure 1). At the plant level, it seems that the relative organ sizes play an important role in maintaining the internal homeostasis between the supply and requirement of various substances (e.g. Brouwer 1962). However, also the shape of the grown organs can be important.

The morphology of the leaves can be quite variable depending on the growth conditions (e.g. Kellomäki and Oker-Blom 1981; Ross et al. 1986; see Figure 1, feedback loop from structure to exchange processes). At shoot or crown level, the structure has a central role in determining the intercepted light at a certain point (e.g. Kellomäki and Oker-Blom 1983; Oker-Blom and Smolander 1988; Kuuluvainen and Pukkala 1987, 1989). Interplant interactions do not necessarily have a big importance on the momentary uptake at plant level, since neighbouring exchange sites can intercept a flux that other exchange sites do not. However, the resources that are available for structural growth of different parts in the long run can be very different. This is because the material requirements of forming different architectural patterns are different.

The growth of an above ground part of a tree consists of leaf formation, associated axis elongation and secondary thickening of these axes and previously formed structure. Carbon and nutrient availability, i.e. the input and output processes, determine the growth of leaf at the coarsest level. However, also stored compounds play an important role in growth, especially in matching the rates of input/output processes with those of the growth processes (e.g. Gordon and Larson 1968). The growth of leaves seems to be the fastest close to the best local source of water and metabolites (see review by Dale 1988).

At the cell level, the growth is associated with cell turgor. The needs of maintaining turgor and allowing the cell wall to loosen and extend place conflicting demands on the growth of cells (Dale 1988). The control of these processes is still rather poorly known but the osmotic regulation seems to have a central role (e.g. Cosgrove 1986; Dale 1988).

Length growth can either be influenced by the conditions of the previous and the present summer (determinate growth, e.g. Mikola 1950), or the growth can be determined by the environment of the most recently formed mature leaves (indeterminate growth, e.g. Dickson and Isebrands 1991). Needles and connecting vascular system develop simultaneously and can be regarded developmentally and functionally a single organ (Larson 1969; Watson and Casper 1984). Similarly, developing leaf is intimately connected to the stem vasculature in trees with indeterminate growth (cf. Dickson and Iserbrand 1991).

Cambial cells resume their activities as dormant buds start developing. Auxin has an important role in reactivating hardwood cambia (Savidge and Wareing 1981) although also cytokinins play a role in the initialisation of vascular differentiation (Aloni 1991). Savidge (1991) has shown that auxin or sucrose availability is not controlling the biosynthesis of coniferin which is the main precursor of lignin in conifers. Therefore he suggests that the woody growth is controlled by the interaction of auxin and cytokinins. The growing parts, such as shoot apex, buds but also developing leaves seem to be the main source of auxin in plants (Sembdner et al. 1980) but also the old leaves of the conifers produce it (Savidge and Wareing 1981; Savidge 1988).

Aloni and Zimmermann (cited by Aloni 1987; Roberts et al. 1988) proposed a hypothesis that the rate of conduit differentiation would depend on the amount of auxin that the differentiating cells receive. The distance from the auxin source to the differentiating cell would determine the auxin concentration at that place. The rate of cell differentiation determines the final size of a conduit; because cell expansion ceases after the secondary wall is deposited. Rapid differentiation results into narrow vascular elements while slow differentiation permits more cell expansion. This hypothesis explains quite well the tracheid size differences observed in many species along the height and distance from the pith (see chapter 2.1.2.7).

Old needles have an important role in bringing about the late wood formation (e.g. Larson 1969). Denne and Dodd (1981) conclude that the thickening of late wood cell walls may be caused by shifts in hormonal balances, especially that between gibberellins and auxin (see also Aloni 1991). On the whole, hormonal control seems to affect the woody growth more than the substrate supply. However, Savidge and Wareing (1981) claim that it would be naive to conclude that the only factors involved would be hormonal. As pointed out earlier, the water status of plant can have strong influence on growth. Also, Denne and Dodd (1981) point out that temperature directly affects both the duration and the rate of the cell division.

It seems that growth affects nutrient uptake more than other input processes. This follows from the relatively poor mobility of nutrients, especially that of phosphorus, and their scarcity in natural soils. The adequate distribution of growth can create a balance between the nutrient supply which is largely determined by the growth of the root system, and the nutrient demand, which the growth of the whole tree determines. The idea of the so called functional balance has risen from these considerations (White 1935, cited by Thornley and Johnson 1990, Brouwer 1962).

Ingestad and Ågren (1991) suggest that nutrition mainly controls the fluxes of carbon and nutrients through processes in the shoot; both those affecting the photosynthetic rate (see also chapter 2.1.1.4) and the sink strength of the shoot for carbon. An improved availability of nitrogen would affect the growth of the new shoots resulting into proportionally bigger amount of carbon used to foliage but also because of the close connection between woody and foliar growth, to branches and stem. McDonald et al. (1992) found quite linear ratio between the projected leaf area growth per absorbed nitrogen at given photon flux density for birch (*Betula pendula* Roth.). The slope of this relationship decreased as a function of light availability. The latter was mainly due to changes in the specific leaf area whereas the proportion of leaves from the total biomass remained approximately constant.

Also Clarkson (1985) had the impression that carbon supply is unlikely to be a limiting factor for growth and nutrient transport in well-illuminated plants. However, Chapin et al. (1987) argue that nitrogen acquisition including absorption, translocation and assimilation, forms a major carbon expense (up to 50% of total carbon).

2.1.2.6 Senescence

According to Pell and Dann (1991), maturing, ageing and senescence is a carefully timed sequence of events in plant's life that hormones, at least partially, control. Depending on the organ's stage of development, antioxidants, such as cytokinins, are able to counteract the effect of various oxidising toxic substances, which could cause senescence at later phases of development. So similar environmental stress can have very different effect, depending on the organ's age and growth history (Pell and Dann 1991).

Often the senescence of different organs is described as a function of their age. However, in this respect different plant organs have different characteristics. The woody organs are mainly dead cells (e.g. Kärkkäinen 1985). Thus, the turnover of sapwood to heartwood is not analogous to foliage senescence. Often heartwood formation has been ascribed to ageing phenomena (see Saranpää 1990) but there is also some evidence that it might be more closely connected to crown dynamics and thus functioning of the tree (e.g. Kaipiainen and Hari 1985).

Recently, interpreting trees as modular organisms has started discussion about the autonomy of branches (e.g. Sprugel et al. 1991). Experiments with labelled carbon would tend to indicate that with respect to carbon branches might well be quite autonomous, since there does not seem to be any transport of carbon from young branches into older ones (Isebrands and Dickson 1991). This would mean that the senescence of branch would follow when it is not any more able to produce enough carbon for its self-maintenance (e.g. Isebrands and Dickson 1991). Quite often the mortality of whole trees has been thought to take place with similar manner but at tree level.

Senescence has an important role as a source of nutrients for new growth and in maintaining the balance between the organs that take up and consume water (e.g. Helmisaari 1990; Nambiar 1985; Whitehead 1985). For example Helmisaari (1990) reported that internal circulation of nutrient could supply up to 60 % of the nutrient requirement of new growth in a bole stage Scots pine stand. In addition, senescence together with growth processes determines the architecture of crown (Waller and Steingraeber 1985).

There seem to be genetic limits on the longevity of leaf which together with the environmental conditions can influence the senescence in different parts of tree (Pell and Dann 1991). This favours the nutrient supply of other, remaining parts. However, it seems that unfavourable conditions do not necessarily enhance the proportion of nutrients retranslocated from the senescing structures (e.g. Nambiar 1985). The total amount of dying foliage, though, can be connected to environmental stress (e.g. Jukola-Sulonen et al. 1990).

2.1.2.7 Functional interpretations of the woody structure

Chapter 2.1.2.5 indicated a close relationship between the foliage and wood growth that the hormonal signals from existing and developing leaves mainly control. Development of a tight control at tree level could indicate that the processes bringing about woody growth have been critical for a success of trees in the evolution. This is not surprising, since the position, mechanical support and the material transport between foliage and fine roots depend on the woody structure and on the closely connected phloem.

The interpretation of woody structure satisfying some functional requirements has quite a long history. Already in his notes, Leonardo da Vinci put forward the concept that has later been called the pipe model theory (Shinozaki 1964 a, b; Zimmermann 1983). Since those days the woody structure has been examined from the mechanical support point of view (Schwedener 1872 and Metzger 1896; cited by Ylinen 1952), from the water conductance point of view (e.g. Jaccard 1913, cited by Zimmermann 1983, Huber 1928) and from the assimilatory capacity point of view (Pressler 1865, cited by Assmann 1970).

King and Loucks (1978), King (1981) and Morgan and Cannell (1988) among others have studied the implications of mechanical support requirement on shoot and tree structure more recently. On the other hand, e.g., Zimmermann (1983), Ewers and Zimmermann (1984), Tyree and Sperry (1989) have paid attention to the water transport properties of wood. Although the pipe model theory of wood was initially proposed as purely a morphological model, it has also been considered as an approximation of structural adaptation to certain water availability and transpiration conditions (e.g. Jarvis 1975, cited by Whitehead 1985; Waring et al. 1982; Hari et al. 1986a).

The water flow in plants is generally explained by the so called cohesion theory originally proposed by Askenasy (1895) and Dixon and Joly (1894) (cited by Gregory 1977). This can be described with the Hagen-Poisseule equation (Mäkinen, pers. comm.). The most critical weakness of the approach is that it does not consider the resistance caused by the pits joining tracheids together nor that caused by the cell walls (Carlquist 1988). The difference between calculated resistance with Hagen-Poisseule equation and that measured seem to differ somewhat depending on the species in question. Pothier et al. (1989) measured resistance that was over two folds greater than the values calculated with the equation for Jack Pine (*Pinus banksiana* Lamb.). Haskins and Ford (1990) suggested that for these reasons one should consider also other relationships to describe the water flow through tracheids.

Although the Hagen Poisseule equation does not necessarily describe the water flow in real wood, it helps to evaluate aspects of woody structure that are important in determining the flow of water in the plant. The water flow through wood depends on a) the vessel lumen diameter, b) the size and quantity of inter tracheidal pits especially in conifers and c) the length of the tracheids in conifers and the number of pits in the tracheidal walls. Points a) and b) seem also to be connected to the size of tracheids. On the other hand, as pointed out by Carlquist (1988) and Tyree and Sperry (1989), wider vessels need not to be more efficient in water transport in nature since cavitations seem to take place more readily in such vessels than in smaller ones. This might be an important factor, especially in trees growing in hard winter where embolism due to freezing is a risk (Tyree and Sperry 1989).

The distribution of tracheid sizes in conifers such as Scots pine seems to follow clear patterns: a) both tracheid length and diameter first increase from pith outwards and then stabilise b) from the top of the tree downwards the length and diameter of the tracheids increase up to a certain height that seems to move slowly upwards as the tree grows and c) within tree ring the lumen diameter generally decreases from early wood towards late wood (Sanio 1872; Dinwoodie 1961; Bailey 1958; Burley and Miller 1983). The ratio between early wood and late wood also changes so that it remains rather stable within the living crown but increases considerably when going downward from the pruning height (Larson 1969, Hari, pers. comm. (Department of Forest Ecology, University of Helsinki)). In addition to these trends, there seems to be a concentration of smaller tracheids where branches fork from the main axis (e.g. Zimmermann 1983). This observed pattern coincides quite well with the hypothesis by Zimmermann and Aloni (see Aloni 1987) on the role of auxin in xylem cell differentiation.

One might expect that water conductivity within stem and branches in different positions would be very different based on the observations on the tracheid size distributions. The early work of Huber (1928) and subsequent measurements by several other people have demonstrated that this is the case (Zimmermann 1983, Ewers and Zimmermann 1984; Tyree et al. 1987). The water conductivity per supplied leaf mass shows manifold variation between the smallest twigs and the main stem (e.g. Tyree et al. 1987). On the other hand, clear constriction points to water flow seem to exist at the junctions where branches fork from the main axis. These observations lead Zimmermann (1983) to hypothesise that the main axis of a tree is preferred in the water transport. The most distal twigs would become cavitated first in unfavourable conditions of excess demand. This would hinder the water flow to those and guarantee a higher flow to the main axis.

The storage of water in the woody compartments can be an important factor balancing sharp diurnal and even longer term variations in the water demand and uptake (Jarvis et al. 1981; Whitehead 1985). There are clear elastic changes in the woody tissue that are connected to transpiration but with lag that would indicate the storage effect (Mäkinen, pers. comm.). Whitehead (1985) suggests that the sapwood proportion would be higher in the trees adapted to more continental climate than in those adapted to more maritime climate. The higher storage capacity in continental trees would enable them to function even at dry summer periods.

2.1.3 The role of growth processes in tree functions

The tree functions at any moment consist of various input/output reactions that are influenced to varying degree by the past conditions through the internal substance concentrations, the state of the biochemical "machinery", the structure and the genetic information. The responses of the input/output reactions to the environment are relatively well known as the brief discussion on tree functions from the growth point of view indicated. However, much less is known on control mechanisms that match the various, simultaneously occurring flows that bring about the internal "state" of the plant. Also the nature of the feedback from these internal processes to the exchange processes is not yet known. The same applies to growth reactions that are the main sinks of the materials taken up, and also to senescence reactions that can be an important source of resources for new growth.

These growth reactions produce the structure of plants. As the discussion on the water transporting properties of wood indicated, the structure determines the limits for the flux of materials through a certain part of the system at a given period. Thus growth can be viewed as plant's means of matching structure with function. The study of the control mechanisms of growth face many methodological problems since the growth processes are slow and the structure of the plants always reflects the past conditions to a great extent. However, the stable internal material combinations in the plants (e.g. Davidson 1969; Hunt 1975, Richards et al. 1979) suggest that growth (and senescence) of different parts of trees must be such that structural limitations do not prevent the formation of balance between the net intake of materials and their consumption.

2.2. Stand growth model

2.2.1 The main assumptions of the model

Tree stands are interpreted as a spatially and temporally hierarchical system in which the vegetation acclimates to its surroundings at very different scales both in time and space. Material fluxes between plant and its environment change as the environmental conditions change. Growth reacts slowly to these changes but it also changes the material flows between the plant and its surroundings. Thus, the role of growth processes is identified as plant's means of matching the structure with function. Temporally this is a rather aggregated process but spatially growth affects virtually all levels of hierarchy.

The applicability of the presented theoretical framework to growth analysis cannot be tested directly. Further definitions of quantitative relations that occur in forest stands are needed. However, as yet, our knowledge on the control of the internal processes and the feedback loops between different levels of hierarchy is somewhat sketchy (see Chapter 2). de Wit and Penning de Vries (1983) pointed out that our knowledge on the functioning of the communication systems of plants is still too limited to be able to include it into the models at mechanistic level. This means that further assumptions need to be made when quantitative analyses of tree growth are planned from the presented theoretical framework.

It is assumed that the control of material producing exchange processes and material consuming growth processes is such that the internal state and the internal processes per unit volume remain stable. Material exchange processes depend on the momentary environmental conditions but growth depends on the material fluxes between plant and its surroundings over time periods. Therefore the stable internal state can only be expected over time periods that are long enough to facilitate acclimation of growth.

The growth of different structures would thus need to match the consumption of different materials with the uptake of the same materials. So, I assume that the growth processes consume resources and create new material exchanging organs in such a manner that the internal concentrations of resources within the plant organs remain constant or depend on the resource availability according to a known function. This assumption follows the idea of the functional balance principle presented by Brouwer (1962) and can be at least partially justified by empirical observations (e.g. Davidson 1969; Hunt 1975; Richards et al. 1979).

The assumptions of internal states that can be variable within a year but remain constant from year to year facilitate estimations on the annual flow of different materials per unit surface area. In other words, the structure changes so that the flux through unit surface area remains the same at annual bases in similar climatic conditions. Furthermore, the basic functions of a tree per unit volume are independent of its age but they change due to changes imposed to the environment by the stand development. Then the uptake rate per unit of exchanging organ depends both on the total flux of material and energy reaching the stand and on the competition effect. The latter naturally depend on the distribution of exchanging organs in space (see Chapter 2.1.2.2).

The main material flows in ecosystems are those of carbon, nutrients and water. The carbon and nutrient fluxes are treated explicitly. The nutrient limiting growth represents all of them, as others are assumed to be obtained in necessary quantities. Water flows are considered only implicitly. There is a clear connection between photosynthetic production and the transpiration, on one hand, and water uptake and transpiration, on the other hand. Thus, a simplification is used that describes the water flow through the effects on the photo-production and through the structural requirements to maintain the required transport between different parts of tree. The assumption of a constant ratio between the water-conducting wood and the water-transpiring foliage describes this relationship (e.g. Hari et al. 1985; Valentine 1985; Mäkelä 1986; Nikinmaa 1987).

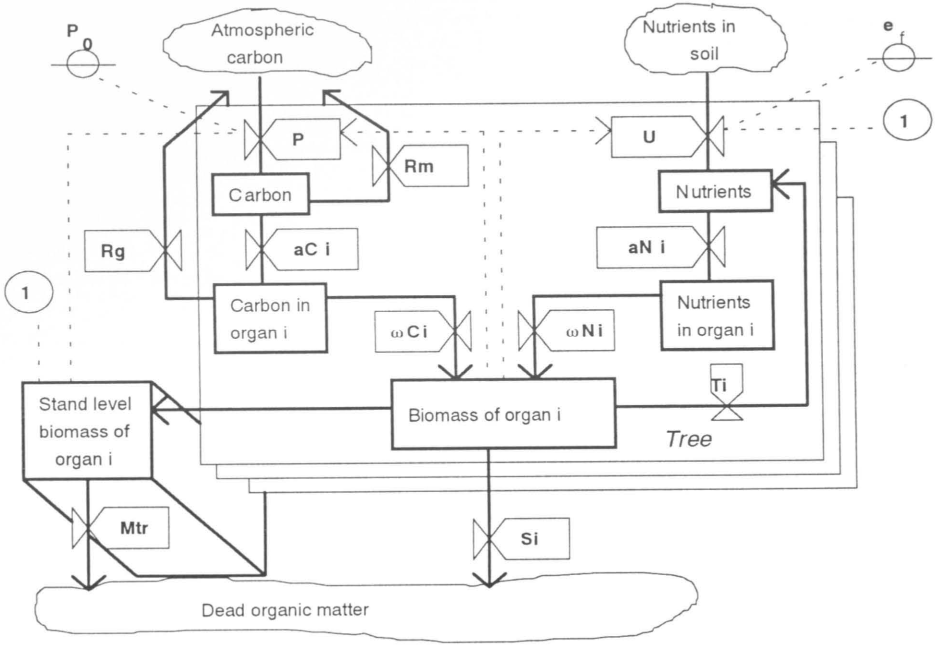

Figure 2. A schematic presentation of the stand growth model. For the sake of clarity only the material flows (solid lines) and stand level information flows are presented . P_0 and e_f stand for the annual uptake of carbon and nutrients per unit mass of uptaking organs under no competition, R_m and R_g are the maintainance and growth respiration, $a_C i$ and $a_N i$ allocation of carbon and nutrients to structural growth of biomass compartment i, w_{Ci} and w_{Ni}, conversion efficiency of carbon and nutrients into the biomass of compartment i, W_i, the biomass compartments (i= needles, branches, stem, transport roots and fine roots), T, retranslocation of nutrients, S_i , senescence of biomass compartments and Mtr mortality of trees. In the present version the processes aCi, ωCi, aNi and ωNi are assumed to take place so that C:Nutrient ratio in each biomass compartment is a compartment specific constant and the structural regularities between different biomass compartments remain constant (see Chapter 2.2.3).

A model based on the material budgets and systems analyses presented by Hari et al. (1982) and Mäkelä and Hari (1986) is developed further to analyse the implications of these assumptions on forest growth. Stand level dynamics are described with growth and mortality of trees. These are further divided into functionally different biomass compartments. These are the state variables of the model. Figure 2 presents the overall frame of the model.

The exact formulation of the used approach is presented in the continuation. First the basic formulations of the approach are presented. From these common principles two different models that operate at different hierarchy levels are constructed and their main differences are presented as the last point of this chapter. Appendices 1 and 2 present those equations of the models that do not appear in the text. They are mainly to derive the dimensional changes from the presented considerations. Appendices 3 and 4 present the general structure of the constructed models and the order in which the different equations appear in them.

2.2.2 *Stand structure, material balances and input-output processes*

Stand can be considered to consist of trees with certain architectural characteristic represented by the average tree in the simulations (e.g. Mohren 1987). Alternatively, one can consider individual trees, their architecture and distribution within a stand (e.g. Grace et al. 1987b; Oker-Blom et al. 1989). Huston et al. (1988) suggest that models operating at tree level would be more realistic since they could include both genetic and environmental variations between individuals and because local interactions mainly affect the organisms. From the management point of view, the dynamics of tree size distribution is one of the most interesting questions, favouring tree level models. However, modelling spatial dynamics easily results into very complicated and time consuming solutions.

As a compromise between these two approaches, the stands can be described with trees belonging into different size classes (Hari et al. 1982). Then average trees represent the trees of each size class, j, in the simulations. The stand level biomass, Y_{tot} (kg/ha), is the sum of the biomass of the representative tree of each size class, W^j_{tot} (kg), times the number of stems, N^j (1/ha), in the size class. The yearly change of the biomass of a stand is then:

$$Y_{tot}(k+1) = \sum_j \left(N^j(k) + \Delta N^j(k)\right) \left(W^j_{tot}(k) + \Delta W^j_{tot}(k)\right) \tag{1}$$

In the following the equations necessary to calculate the changes in the biomass of trees are presented. These include the formulation of the material balance of trees, the presentation of the input/output processes and the presentation of how the distribution of resources is derived from the conditions of balanced internal state and balanced structure. The growth of different biomass compartments is first derived at the shoot level and the description how the whole tree growth can be calculated from the shoot level premises follows thereafter. As the last point of the tree mass balance, the senescence of the different biomass compartments is treated. After the mass balance of one tree is described the equations describing the change of the number of stems are treated.

The material balances of a stand facilitate the exact formulation of the presented principles. Consider that trees consist of different functional biomass compartments of needles, n, branches, b, stem, s, transport roots, tr, and fine roots, f. We can denote the mass of each biomass compartment i of trees of size class j by W^j_i (kg). Let us denote the annual growth and senescence of the same biomass compartments by G^j_i and S^j_i (kg). Now we can write the mass changes at tree level as:

$$W^j{}_{tot}(k+1) = \sum_i G^j_i(k) + W^j_i(k) - S^j_i(k) \tag{2}$$

The annual growth of a tree depends on annual material intake, I (kg), and loss O (kg). If it is assumed that there is no storage of material on annual bases, or that changes in it are small, the growth of a tree is directly proportional to the difference between intake and loss. Let us now consider the growth of one tree. The growth of a biomass compartment i, G_i, of a tree is naturally proportional to the amount of materials distributed to that compartment, α_i. If no storage is assumed, the sum of these allocation proportions is 1. Let us further denote the conversion efficiency of material to structure by ω_i (kg dm/ kg C or N, where C and N refer to carbon or nutrients, respectively and dm refer to dry matter). The following equation gives the material balance of one tree:

$$\sum_i \frac{G_i}{\omega_i} = \sum_i \alpha_i (I - O) = I - O \tag{3}$$

The annual input/output reactions considered in the model are photosynthetic production, P (kg C), respiration, R (kg C), nutrient uptake, U (kg N) and nutrient retranslocation, T (kg N). The conversion efficiency of carbon and nutrients into structure is specific for each biomass compartment and is assumed constant. The bases for its calculation are presented together with the treatment of the respiration costs. The proportion of resources distributed to biomass compartment i, α_i, is calculated from the assumptions of balanced internal state and it is variable. Chapter 2.2.3 treats the distribution of growth between the biomass compartments.

The photosynthetic production by a tree is a function of the potential annual production without the shading effect, P_0 (kg C/kg dm), and the total shading effect that the trees of the stand exert on the tree in question (e.g. Hari et al. 1982). The potential production depends on the internal state of the tree and the environment of the location above the stand. It is assumed that from the above ground environmental factors affecting photosynthetic production, only the light availability would be changing significantly within the canopy and would be influenced by the stand development. Thus, it describes the within canopy interaction between trees (e.g. Hari et al. 1982). In this approach it is also assumed that the spatial interactions within the canopy can be reduced to one dimension. The position of a tree within a stand would then be determined solely by the vertical position of the foliage in the canopy (Hari et al. 1982)

The water and nutrient availability have an effect on the photosynthetic production. They are assumed to take place through the internal states and would thus reflect on the potential production. The annual cycle affects the photo production, especially in the spring, and needs to be considered when the annual photosynthetic production of the unshaded conditions is calculated (see also Chapter 2.1.2.3). Water availability can have substantial effect on the photo production during the growing period even in the northern latitudes of Finland (Korpilahti 1988). For the model calculations the potential photo-production, P_0, is determined based on the field measurements of photo-production and of the annual variation of the environmental conditions in Southern Finland (Korpilahti 1988; Hari et al. 1991).

The degree of interaction, ι, at any point in the canopy is the photosynthetic production over a period of time at that point divided by that of the unshaded conditions (Hari et al. 1982). The interaction can be derived from the time integral of irradiance only since it is assumed that the photosynthetic light response would remain constant in the canopy (e.g., Hari et al. 1989). The assumption of horizontally homogeneous canopy simplifies the treatment, i.e. the degree of interaction, ι, depend only on the shading leaf area, $Y_n(z)$ (kg/ha), above the point in consideration (z). Kellomäki et al. (1980) determined an empirical relationship for the degree of interaction for Scots pine. It is expressed in the following form (Hari et al. 1982, simplified by R. Sievänen, pers. comm. (Finnish Forest Research Institute)):

$$\iota(z) = 1 \Big/ \left(1. + 0.026\left(Y_n(z)^{0.58}\right)\right) \tag{4}$$

The foliage biomass above point z in the canopy ($Y_n(z)$) is the sum of the foliage masses of all the trees in the different size classes. The photosynthetic production by a tree at a year k, P(k) (kg), is then (Hari et al. 1982):

$$P(k) = P_0 \int_{h_{\min}}^{h_{\max}} \chi_j(z)\, \iota(z)\, dz \tag{5}$$

where h_{max} and h_{min} are the maximum and minimum heights of the canopy (in meters) and χ_j, (m^2/m) is the needle area density at height z of trees in the size class j.

Respiration is divided into maintenance and growth respiration according to the approach suggested by Penning de Vries (1974) (see also Chapter 2.1.2.3). Growth respiration per unit growth of tissue is calculated from the type of structure and the composition of different chemical compounds in the structure (Penning de Vries et al. 1974; Mohren 1987). The conversion efficiency, ω_C (see Equation 3) of the photosynthesised carbon to dry matter could then be calculated as presented by Mohren (1987) and is used as a parameter value in the model.

Maintenance respiration depends on the metabolic activity of cells in the tissue (e.g. Penning de Vries 1974). The protein and mineral contents of the tissue mainly determine the rate of respiration. The respiration rates can be determined for different tissues based on their mineral and protein contents following the method described by Mohren (1987). The maintenance respiration of a tree at year k, R(k), (kg), is:

$$R(k) = \sum_i r_{mi} W_i \tag{6}$$

where r_{mi} (kg C/kg dm) is the annual respiration loss per unit weight of biomass compartment i.

The annual respiration loss is calculated assuming that the tissue specific rate is only affected by the temperature. For the temperature effect, a so called Q_{10} value of 2 is used, i.e., 10 degree rise in temperature would double the respiration rate (e.g. Landsberg 1986). It was found out in the calculations of the temperature effect that the mean temperature of the active period could be used instead of daily mean temperatures, considering the uncertainty that is involved in the tissue specific respiration rate (see Chapter 2.1.1). The mass specific annual respiration rate for biomass compartment i, r_{mi} (kg C/kg dm), is:

$$r_{mi} = r^*_{mi} \cdot E \cdot 2^{\left(\bar{T} - T_b\right)/10°C} \tag{7}$$

where r^*_{mi}, (kg C/kg dm/h), is the respiration rate at the chosen base temperature, E, (h), is the extent of the active period, $\overline{T}$, (°C), is the average temperature of the active period and T_b, (°C), is the base temperature at which the respiration rate has been determined.

Yearly nutrient uptake by the root depends on two factors: a) the site dependent annual nutrient uptake by unit mass of fine roots grown per year without competition effect, e^*_f (kg N/kg dm), and b) on the competition effect that can be described using a negative exponential function with respect to the total mass of fine roots in the stand, Y_f (kg/ha) (Fitter and Hay 1987). It is further assumed that the fine roots would not compete with each other if the density of fine roots, Y_f, in the stand is lower than a set threshold density, D_r. This threshold density is also the density at which the roots of one tree are growing. From these assumptions the specific annual nutrient uptake by unit mass of fine roots, e_f (kg N/kg dm), is:

$$e_f = \begin{cases} e^*_f, & \text{when} Y_f \le D_r \\ e^*_f \cdot g(Y_f), & \text{when} Y_f > D_r \end{cases} \tag{8}$$

where g is a function describing the decrease in the nutrient uptake efficiency as a function of total fine root biomass of the stand, Y_f. The actual shape of the functions used is presented in the Appendices 1 and 2.

2.2.3 *Distribution of growth based on balanced internal state*

A constant internal composition of the active tissue is a simplification of the balanced internal state. The changes in the size of the tree structures reflect changes in the flow rates between the plant and its environment at annual bases. The balance between the woody structure and the internal state is assumed when the transport capacity of the wood matches the in- and outflows at the exchanging sites. An approximation of this is the constant ratio between the amounts of water transpiring foliage and the cross-section of water transporting wood (e.g. Hari et al. 1985; Valentine 1985 1987; Mäkelä 1986 1988; Nikinmaa 1987; Ludlow et al. 1990).

According to Equation (3), the growth is the difference between the in- and outflow. The assumption that active tissue has a constant composition gives growth that is linearly proportional to the amount of resources distributed to that compartment (e.g. McDonald et al. 1992). We can substitute the annual nutrient uptake, U (kg N) or photosynthetic production, P (kg C) for the input (I) in Equation (3). On the other hand, annual retranslocation of nutrients, T (kg N) or annual respiratory loss, R (kg C) can be substituted for the output (O) (retranslocation can be viewed as a negative output). Then we need to note the distribution and conversion efficiency of nutrients and carbon into structure of biomass compartment i by α_{Ni}, α_{Ci} and ω_{Ni}, ω_{Ci}, where N and C refer to nutrients and carbon, respectively. Now, we can write growth of biomass compartment i, G_i, (kg), in terms of nutrient or carbon balance as follows:

$$G_i = \alpha_{Ni}\omega_{Ni}(U - T) = \alpha_{Ci}\omega_{Ci}(P - R) \tag{9}$$

Let us substitute fine root mass times the nutrient uptake efficiency, e_f, from Equation (8) for U. Let us also assume that nutrients retranslocate only from senescing needles and that the amount of nutrients retranslocated, ξ (kg N/kg dm), is constant. We can now write growth (Equation 3) as a function of nutrient flows as follows:

$$\sum_i G_i/\omega_{Ni} = e_f\left(G_f + W_f - S_f\right) + \xi S_n \text{ ; i=n, b, st, tr} \tag{10a}$$

which reads after evaluating the summation and rearrangement:

$$\begin{aligned} &G_n/\omega_{Nn} + G_b/\omega_{Nb} + G_{st}/\omega_{Nst} + G_{tr}/\omega_{Ntr} \\ &= \left(e_f - 1/\omega_{Nf}\right)G_f + \xi S_n + e_f\left(W_f - S_f\right) \end{aligned} \tag{10b}$$

In the continuation it is assumed that S_f equals W_f so that only the fine roots formed during the same year are active in the nutrient uptake. On average they take up nutrients the amount described by the root specific uptake rate during their life span in the year. So, in fact S_f can be greater than W_f but this excess is taken into account in the annual nutrient uptake by unit mass of fine roots, e_f. The latter depends on the initial fine root mass of the stand, Y_f, that is the same as the fine root mass growth of all the trees of the previous year since S_f equals W_f. This approach is adapted, since the growing roots are generally most efficient in nutrient uptake (e.g. Clarkson 1985) and the annual turnover rate of fine roots seems to be very high (e.g. Persson 1980).

The reciprocal of the conversion efficiency of nutrients, π_i (kg N/ kg dm) describes the nutrient concentration of the tissue in question since the conversion of nutrients is a linear function of available nutrients at the biomass compartment. This can be substituted for ω_{Ni} in Equations (10 a and b). The annual growth of fine roots as a function of growth of other compartments yields:

$$G_f = \frac{\sum\limits_i \pi_i G_i - \xi S_n}{e_f - \pi_f}, \text{ i = n, b, st, tr} \tag{11}$$

In deriving Equation (11), the equality $W_f = S_f$ has been taken into consideration.

The assumption of a constant ratio between the water conducting wood cross-sectional area and the amount of needles above the cross-section, ε_i,(m^2/kg), can describe the woody growth as a function of foliage growth. The change of the size of the woody structure is a function of the change in the amount of the foliage, G_n–S_n (kg), the annual turnover of sapwood into heartwood, H_b, H_{st}, H_{tr}, (kg), the length of the woody structure, l_i (m), and the density of woody material, γ_i (kg/m^3), if the ratio remains constant from year to year (e.g. Hari et al. 1985). Since the ratio between the cross-sectional area of water conducting wood and foliage biomass seems to change at different parts of the transport path (Hari et al. 1986a) the annual growth of branches, stem and transport roots per growth of needles (assuming no length growth) becomes (e.g. Mäkelä 1990b):

$$G_b = \varepsilon_b \gamma_b l_b (G_n - S_n) + H_b \tag{12}$$

$$G_{st} = \varepsilon_{st} \gamma_{st} l_{st} (G_n - S_n) + H_{st} \tag{13}$$

$$G_{tr} = \varepsilon_{tr} \gamma_{tr} l_{tr} (G_n - S_n) + H_{tr} \tag{14}$$

where n, b, st, and tr stand for needles, branches, stem and transport-roots.

The growing and senescing foliage is attached to the "pipeline" at different positions in Scots pine. So the average length of the pipe from fine roots to senescing foliage, l_s (m) and the average length of new "pipe" in shoots, Δl_b (m), need to be considered. Then the annual growth of wood for needles growth at certain branch q is:

$$G^q_b = \varepsilon_b \gamma_b \left[\left(\Delta l^q_b + l^q_b\right)G^q_n - l^q_{sb} S^q_n\right] + H^q_b \tag{15}$$

$$G^q_{st} = \varepsilon_{st} \gamma_{st} l^q_{st} \left(G^q_n - S^q_n\right) + H^q_{st} \tag{16}$$

$$G^q_{tr} = \varepsilon_{tr} \gamma_{tr} \left[\left(\Delta l_{tr} + l_{tr}\right)G^q_{tr} - l_{tr} S^q_{tr}\right] + H^q_{tr} \tag{17}$$

where l_b, (m), is the average length of the transport path to the new shoots. The Δl_t, (m), stands for the average length of new transport roots.

We can place Equations (15)–(17) to Equation (11), to get the growth of fine roots as a function of the growth of foliage. Then we can place the growth of fine roots and the woody biomass compartments written as a function of the growth of foliage from Equations (11) and (15)–(17) to Equation (3). The equation can be rearranged so that the terms including the growth of foliage are written on the left hand side. Those terms that do not include foliage growth are summed with the net photosynthetic production term on the right hand side. These terms include those associated with the senescence of foliage and those describing the heartwood formation. Then we can separate the growth of foliage as a common term on the left side and divide the right hand side with the resulting multiplier.

The growth of foliage of branch q is thus a function of the difference between the photosynthetic production and the respiratory losses of the branch, $(P\text{-}R)^q$, the senescence of foliage, the heartwood formation, the nutrient uptake, and the transport path length and the length growth. It is also assumed that the condition of Equation (3) would hold for each branch, i. e. the branches and the structure in other parts of the tree required for their physiological and mechanical support would form independent units, as Watson and Casper (1984) have suggested. These considerations yield Equation (18) (See page 22).

In Equation (18), the respiration of the branch q, R^q, (kg C), is the maintenance respiration of the whole structure required to support that branch. ω_{Ci}, (kg dm/kg C) refers to conversion efficiency of carbon into structure and π_i, (kg N/kg dm) is the concentration of nutrients in the different structures. In the sum sentences, i refers to branches, stem and transport roots, i.e. the woody structure and Δl^q is the average length growth of the new shoots in a branch or new length growth of transport roots. The length growth of stem, Δl^q_{st}, is naturally zero for all branches. The top of the tree can be treated as a branch down to the whorl of branches above which there are needles attached to the stem. l_{si} is the length of transport path to senescing needles. This differs from l_b in branches but is the same as l_i in stem and in transport roots.

The growth of other biomass compartments to support the needles of branch q, G^q_i, is obtained by placing the foliage growth of branch q, G^q_n, into Equations (11) and (15)–(17). The growth of the needles and the associated structure requir-

$$G_n^q = \frac{(P-R)^q + S_n^q\left(\sum_i \varepsilon_i \gamma_i l_{si}^q / \omega_{Ci} + \frac{\xi + \sum_i \pi_i \varepsilon_i \gamma_i l_{si}^q}{(e_f - \pi_f)\omega_{Cf}}\right) - \sum_i H_i^q / \omega_{Ci} - \frac{\sum_i \pi_i H_i^q}{(e_f - \pi_f)\omega_{Cf}}}{\omega_{Cn}^{-1} + \sum_i \varepsilon_i \gamma_i (\Delta l_i^q + l_i^q) / \omega_{Ci} + \frac{\pi_n + \sum_i \pi_i \varepsilon_i \gamma_i (\Delta l_i^q + l_i^q)}{(e_f - \pi_f)\omega_{Cf}}} \tag{18}$$

ed to support them of the whole tree is the sum of the growth of needles in individual branches and in the top of the tree and the sum of structures required to support the needles of individual branches.

The first parenthesis in the numerator in Equation (18), (P-R), gives the net production for new growth, the second positive term gives the resources that come to reuse from dying needles, i.e. the internal circulation of nutrients and structure and the negative term represents resources lost due to senescence of structures. In the denominator are the transformation efficiencies of carbon to needles, the cost of building the woody structures and the cost to maintain the nutrient balance associated with a unit of needle growth. As the tree size increases, the relative importance of senescing foliage as a releaser of nutrients and structure increases. Similarly when the nutrient uptake rate is low, the senescence of foliage and other structures have more importance in releasing nutrients. From Equation (18) it follows that increased senescence of foliage tends to increase foliage growth and decrease woody growth and vice versa, i.e. the structural balance between foliage and woody structure is maintained.

Equation (18) is not allowed to have negative values but branches die when the foliage growth is zero. This follows when the sum of net production and the release of resources by dying needles is smaller than the term associated with the senescence of structure. So it follows from Equation (18) that new needles may grow even if the photo-production of a branch is smaller than the maintenance respiration cost of supporting the branch and all the associated structures in stem and roots. The branch can, in a way, trade the maintenance cost of structures with the release of supporting structures in stem and roots by the dying needles.

Other way of saying above is that the release of transport capacity by the dying needles decreases the carbon export requirement from the branch to the support of infrastructure in the stem and roots. This is because the existing structure can support bigger proportion of the new needle growth than would otherwise be the case. According to Equation (18) there could be needle growth even if the maintenance cost to support only the structure within the branch is bigger than the photo-production of the branch. The work with ^{14}C has indicated that carbon is not translocated to the old branches from other parts of the tree (e.g. Iserbrands and Dickson 1991). So the transport capacity release can only decrease the "investment requirement" from the branch to the woody structure. If more woody structure is released that can be utilised by the branch, the extra "recirculated structure" can benefit only other branches. The carbon resources that are thus freed seem to be used by other branches and are not translocated for the use of the branch where dying needles were.

The growth of trees can be treated at the level of shoot and branch growth. The growth of these units seems to be determined by the local environment of the exchanging sites of the units and their relative position within the tree. The reuse of existing transport structure seems to be a strong determinant of shoot and branch growth. Through it the past history of the tree as a whole has a strong influence on the growth performance of individual shoots.

2.2.4 Crown dynamics

The factors determining the length growth of the pipeline is not treated in Equations (15)–(17). King and Loucks (1978) have demonstrated that the length of the shoot and its diameter are linearly proportional if the structure is mechanically optimal. Several people have measured such ratio from different species (for review see Cannell et al. 1988). The pipe model considerations give the same length/diameter relationship for the shoot if the needles are uniformly distributed on the shoot surface. Connecting this principle with the pipe model allows us to write the length of new shoot , l_{sh}, (m), as a function of foliage growth.

$$l_{sh} = \eta\left(\varepsilon_{sh}G_{nsh}\right)^{\frac{1}{2}} \tag{19}$$

thus

$$G_{wsh} = \eta\gamma_{sh}\left(\varepsilon_{sh}G_{nsh}\right)^{\frac{3}{2}} \tag{20}$$

where η, is the ratio between the length and diameter of new shoots, ε_{sh}, (m^2/kg), is the ratio between the wood cross-sectional area and the foliage mass and γ_{sh}, (kg/m^3), is the density of wood of the new shoots, respectively, and wsh and nsh refer to shoot wood and shoot foliage.

In addition, one needs to consider the forking effect at the level of new shoots. There is a clear trade-off between the cost involved in building the mechanical and physiological supporting structure in the new shoot and the amount of carbohydrates produced by the foliage of the shoot (e.g. Ford 1985). The Equation (20) shows that the supporting cost of shoot rises exponentially as its needle mass grows. Thus, it is more economical from the carbon budget point of view to distribute the same amount of needles among many shoots. However, many shoots close to each other may increase self shading and decrease the average productivity of the needles.

Equation (20) can be modified to consider the above aspects. A general value, n, is given for the exponent in the equation. If it has value 3/2 then all the needles will grow on the same shoot. A decreasing value implies increased forking. However, only values above one are possible in the equation. When shoots are small, then practically the same solution is obtained for all the exponent values. The effects of the exponent value start to show only in better growing conditions when shoot growth is big.

At the branch level, we are talking about the average shoot growth. Thus we would need to know the size distribution of shoots. Simplest way is to assume that the average needle growth per shoot is the total needle growth of a branch divided by the number of mother shoots of a branch, ν_q. A simplified equation for the woody growth associated with needle growth in branch q can then be written (there is no differentiation between branch stem and transport roots in the following equation):

$$\begin{aligned} G_w{}^q = {} & \eta\gamma_{sh}\nu_q{}^{(1-n)}\left(\varepsilon_{sh}G_n{}^q\right)^n + \\ & \alpha_w\gamma_w\left(l_w{}^q G_n{}^q - l_{sw}{}^q S_n{}^q\right) + H_w{}^q \end{aligned} \tag{21}$$

where $l_w{}^q$ and $l_{sw}{}^q$ represent the average length of the old pipe from the fine roots to new needles and the average length of the pipe that the senescing needles release to reuse in the branch, respectively, and H_w is the amount of heartwood formation connected to the unit of calculation. Equation (21) is otherwise similar to Equations (15) to (17) but here also the length growth is derived from the foliage growth and no difference is made between wood growth in branches, stem and transport roots.

We can write the growth of tree as a function of the input/output processes at the exchange sites. However, the reuse of transport structure by several needle generations introduces strong tree level influences at the branch level growth as discussed at the end of Chapter 2.2.3. The structure and architecture of trees that reflects the history of the growing conditions influences the growth of branches. This suggests that tree level regulation could be influencing the growth, as well. The growth of an individual shoot would then depend on its own environment, but also on its relative role in the production of the tree and its relative requirement for the supportive woody "infrastructure".

One way to study the distribution of growth between shoots at tree level is to assume optimal use of resources. Existence of such an optimal growth pattern could be justified by evolutionary considerations. Those trees that have been efficient in their use of resources have been able to survive better in competition and have been able to produce more offspring. However, it is not certain to what degree the evolution has been able to bring about optimal growth patterns. Thus, the value of this approach is especially in that it facilitates the analysis of the importance of different factors in the material balance of trees. The optimal distribution of needle growth could now be treated as a problem of obtaining as big production as possible within the constraints set by the construction costs of required organs. For determination of growth to obtain optimal photosynthetic production we can write:

$$\max G_n\left\{\int_{h_{cb}}^{h} P_o\iota(z)\phi(z)(G_n(z)+W_n(z)-S_n(z))dz\right\} \tag{22}$$

while

$$\int_{h_{cb}}^{h_t}(G_n(z)/\omega_n + G_w(z)/\omega_w + G_f(z)/\omega_f)dz = P - R \qquad (23)$$

where P_0 is the potential annual photosynthetic production per unit needle area in unshaded conditions, $\iota(z)$ is the degree of interaction at that height and $\phi(z)$ is the specific needle area at that height.

Let us assume that the growth of new needles does not affect the photosynthetic production of the remaining ones. Then the photosynthetic production of the crown is maximized when the photosynthetic production by the new needles is maximized. The maximisation problem of the photosynthetic production under the restrictions of structural growth can be solved using Euler's method of variation calculus and the multiplier of Lagrange (Elsgolc 1963). The photosynthetic production by the new needles depends on the height density of needle growth, $G_n(z)$, only (the photosynthetic production and restriction are of the form $\int F(z,G_n)dz$ and $\int L(z, G_n)dz$). Thus the optimization problem can be written in algebraic form. The method of the multiplier of Lagrange can be applied to the Euler equation and we get for the restricted optimum of the photosynthetic production by the new needles that $\partial F/\partial G_n - (\partial L/\partial G_n)$ equals zero. The equation can be rearranged so that the ratio between the partial derivative of the sentence to be maximised and the partial derivative of the restriction is constant, λ, (also called the Lagrange multiplier) in the optimal solution, i.e.,

$$\frac{\dfrac{\partial}{\partial G_n}(P_0\,\iota(z)\phi(z)G_n(z))}{\dfrac{\partial}{\partial G_n}\left(G_n(z)/\omega_n + G_w(z)/\omega_w + G_f(z)/\omega_f - P + R\right)} = \lambda \qquad (24)$$

The terms that do not depend on the foliage growth disappear when solving Equation (24), We can write G_w and G_f as a function of G_n as presented in Equations (21) and (11). Then we get the foliage growth as a function of height and λ. The value of λ is determined by the requirement that Equation (23) must hold for the optimal solution.

2.2.5 *Senescence*

Senescence is an important factor determining both the net and gross annual growth of the biomass compartments. Following from the balanced growth principle, the senescence rates have a strong influence on the amount of carbohydrates distributed among different biomass compartments as seen for example in Equation (18). On the other hand, Equation (2) clearly demonstrates the effect of senescence on the net growth of biomass compartments.

The annual senescence of the exchange organs depends on their biomass (fine roots) or on the age of the organs (foliage). The senescence of foliage is naturally associated with the senescence of branches. However, also the release of transport structure in the branches and stem depends on it. The senescence of foliage, S_n, (kg), is calculated as:

$$S_n = \sum_a W_{na}\sigma_{na} \qquad (25)$$

where W_{na}, (kg), is the needle mass of age class a and σ_{na} is the proportion of senescing needles in that age class. Branches die when they lose all the needles, i.e. become positioned below the living crown. Thus the senescence of branches is

$$S_b = \int_{h_{cb}(k-1)}^{h_{cb}(k)} W_b(z) \quad dz \qquad (26)$$

where $W_b(z)$, (kg), is the branch biomass at height z and $h_{cb}(k-1)$ and $h_{cb}(k)$, (both in meters) are the pruning limits the previous year and at present.

The senescence of fine roots and transport roots is simply:

$$S_f = \sigma_f W_f \qquad (27)$$

and

$$S_{tr} = \sigma_{tr} W_{tr} \qquad (28)$$

where σ_f and σ_{tr} are the senescence rates of fine roots and transport roots.

The turnover of functioning transport structure to non-functional heartwood is a more complicated matter since it is a question of mainly dead cells becoming non-functional. In addition, this term has a strong effect on the carbon allocation as can be appreciated from Equations (15)–(18). It is assumed that the turnover would be connected to crown dynamics as suggested by the empirical results of Kaipiainen and Hari (1985). Heartwood formation would be proportional to the death of needles outside the present living crown. The assumption that a certain proportion of dying needles always brings about heartwood formation accounts for heartwood formation in older branches. This yields:

$$H_b = \varepsilon_b\gamma_b\sigma_b \int_{h_{cb}(k+1)}^{h_t(k)} S_n \qquad (29)$$

and

$$H_{st} = \varepsilon_{st}\gamma_{st}\left(\int_{h_{cb}(k)}^{h_{cb}(k+1)} S_n z\, dz + \int_{h_{cb}(k+1)}^{h_t(k)} S_n\sigma_b z \;\, dz\right) \qquad (30)$$

where ε and γ are the ratio between needle mass and wood cross-sectional area and wood density, respectively (see Equations 12–14) and σ_b is the proportion of foliage senescence associated with heartwood formation in branches. $h_{cb}(k)$ is the initial pruning limit, $h_{cb}(k+1)$ is the pruning limit at the end of the period and $h_t(k)$ is the initial height of the tree.

The tree level senescence depends on the carbon budget but is not directly derived from that. Instead, the number of trees per size class decreases as the needle biomass of the representative tree starts to decline (Mäkelä and Hari 1986). The senescence is proportional to the drop of the needle mass according to following function:

$$N_j(k+1) = N_j(k)(1 - m_r\frac{\left(m_t S_{nj} - G_{nj}\right)}{W_{nj}} - \tau_j) \qquad (31)$$

when $m_t S_{nj}$ is bigger than G_n, otherwise

$$N_j(k+1) = N_j(k)(1 - \tau_j) \qquad (32)$$

where m_r is the mortality rate parameter and m_t is the mortality threshold parameter. The first parameter gives the steepness of the decrease of the number of stems and the second parameter sets the limit of how much bigger the foliage senescence has to be in comparison to annual growth to start tree mortality. τ_j refers to a decrease in the number of stems in size class j that disappear for some other reasons such as thinning, etc. In addition to the above equations, the number of stems of a size class is not allowed to become negative.

2.2.6 *The crown and branch level models*

Growth can be calculated either based on the local environment of, e.g., each individual shoot or optimal solutions at the crown level can be sought. The whole tree effects on growth take place through existing structure and the requirement to build new structures for the support of the needles (Equation 18). In the continuation, two different computer models are presented which allow a quantitative examination of the made assumptions.

The crown model

The models used are referred to the crown and branch models. The crown model describes trees with average lengths of branches, stems and transport roots and with a constant crown form between dynamic height and pruning limit growth (see Appendices 1 and 3). The branch model calculates the growth of needles and associated structures at branch or unit height level. The crown form and pruning limit result from this growth (e.g. Nikinmaa and Hari 1990, Nikinmaa 1990).

In the "crown" model, the new length growth was assumed to have a negligible effect on the annual biomass growth in comparison to the thickness growth so it was omitted from the determination of the annual distribution of growth (see Appendix 3). The effect of length growth in terms of carbon takes place the following year when it determines the new length of the woody compartments. Thus, different biomass compartments grow in the manner described in Equations (11)–(14) and (18), assuming that the lengths were average values for trees. The length of the pipe to senescing needles in the stem is equal to the average stem length but in branches the length is that of the branches at the birth of the senescing needles (Equation 15).

The height growth of the crown model depends on the thickness growth (e.g. Sievänen 1992) and the density effect which the light gradient between the upper and lower parts of crowns of trees in different size classes determines. The length growth of branches is proportional to their thickness growth. The length growth of transport roots is derived from the fine root growth and their average density in the soil. The derivation of the pruning limit is a simplification from the optimality approach of the model "branch". It depends on the average photosynthetic productivity of the needles in the crown, the maximum photosynthetic productivity of the needles without shading effect and the light condition at the pruning limit. Additional definitions on how the number of branches and their average length changes from year to year are needed since average values for length were used. Appendix 1 describes the simplifications made in the crown model in more detail.

The branch model

The structure of the branch model is presented in Appendix 4. The branch model treats the height growth of trees with an external function that depends on the maximal annual height growth, the photosynthetic production of a tree and the age of the tree (Mäkelä and Hari 1986). The crown dynamics are derived from the optimality considerations. A special case is applied where the ratio between the photosynthetic production by new needles divided by the cost of construction of needles and the structure required to support them is constant within a crown (e.g. Nikinmaa and Hari 1990, Nikinmaa 1990), i.e.

$$\frac{P_0\,\iota(z)\phi(z)G_n(z)}{G_n(z)/\omega_n + G_w(z)/\omega_w + G_f(z)/\omega_r} = \kappa \qquad (33)$$

In addition, it is required that the construction costs equal the resources available for growth, i.e. the condition of the problem presented in Equations (22) and (23).

It can be shown that if the above ratio is constant also the solution of the optimality problem of Equations (22) and (23) follows. We can move the denominator of Equation (33) to the right hand side of the equality sign. Taking the derivative of both sides with respect of new foliage growth, $G_n(z)$, gives the same solution for constant, κ, as the optimal solution of Equations (22) and (23) gives for the Lagrange multiplier, λ, since the terms that do not depend on $G_n(z)$ disappear. In both cases the value of the constant is determined by requiring that the condition of Equation (23) will hold. Thus the solution of the optimality problem follows from the above principle but the above principle does not necessarily follow from the optimality solution. The acceptable values for those terms that do not depend on the foliage growth are limited in Equation (33).

The principle of Equation (33) says that growth is distributed so that at any height as many units of new resources are obtained per unit of resource invested. If that were not the case, then it would be worthwhile to invest to the height where more is obtained per unit of resources invested until the growth increases the unit cost to the same level as it is in the other parts. The unit cost increases as a function of the foliage mass since the new axis growth depends exponentially on the foliage growth.

Equations (33) can be written as a function of foliage growth. Let us treat the woody structure without differentiating it into branches, stem and transport roots. Then we can write Equation (11) as a function of foliage and wood growth only. On the other hand, the wood growth is treated as a function of foliage growth only in Equation (21). We can substitute these into Equation (33) and get:

$$\begin{aligned}&a_2a_3G_n(z)^n + (1/\omega_n + a_1\pi_n + a_4 l(z) - \\ &P_0\,\iota(z)\phi(z)/\kappa)G_n(z) - a_5 = 0 \qquad (34)\end{aligned}$$

where

$$a_1 = 1/(e_f - \pi_f)\omega_f,$$

$$a_2 = \eta\gamma_{sh}\ \nu^{(1-n)}\,\varepsilon_{sh}{}^n,$$

$$a_3 = 1/\omega_w + a_1\pi_w$$

$$a_4 = a_3\varepsilon_w\gamma_w$$

$$a_5 = a_4 l_s(z)S_n(z) + a_3H_w(z) - a_1\xi S_n(z)$$

$G_n(z)$ can be solved from Equation (34) as a function of the length of the pipeline, $l(z)$, and the constant, κ. An additional condition needs to be introduce apart from Equations (34) and (23) to allow for self pruning of trees. As already discussed at the end of Chapter 2.2.3, the amount of released transport structure can be considerable in the branches where the foliage is decreasing. This can result into a negative cost of woody growth. However, as discussed, the cost cannot be smaller than zero. In fact, in Scots pine foliage growth is always associated with axis growth. Therefore, the cost of woody growth would need to be positive. This limitation is considered in the model in such a manner that there is a maximum limit to the ratio between foliage growth and the total growth of those needles and structure required for them. This is also the same as $\kappa/P_0i(z)\,\phi(z)$. Now, those branches that have high mortality of old needles and poor light conditions have positive foliage growth only if the value of $\kappa/P_0i(z)\,\phi(z)$ is high. By setting an upper limit for the ratio causes them eventually to die.

Appendices 1 and 2 present the additional main equations of the models "crown" and "branch" and Appendices 3 and 4 present the outlines of the models.

2.2.7 Synthesis

The assumption of balanced internal state allows an estimation of the distribution of growth between the different tree compartments as a function of the material flows through exchange surfaces over defined period of time. Rather simple computer models could be designed to make the presented framework operational after making the simplifying assumptions described above. This allows a quantitative testing of the concepts developed through model simulations in various sets of conditions. These results can be compared with observations of the real world behaviour.

In spite of the simple formulation, the presented approach connects the nutrient and carbon flows to the growth of tree. Thus it facilitates the evaluation of their relative importance in the growth phenomena. The description of connection between foliage and woody growth makes the treatment of tree growth at shoot level possible. The immediate environment of the shoots shows up to be an important determinant of their growth. However, also the past history of the trees is an important determinant of the shoot level growth through the internal circulation of structure.

3 Tree and stand growth

3.1 Introduction

One of the main objectives of the present work is to analyse the applicability of the concept of balanced internal state in the studies of tree and stand growth within a material balance framework. The former chapter demonstrated that it is possible to describe growth of trees and stands from those premises with relative simplicity.

The validity of the approach was tested at different levels of the theory. The generality of one of the main assumptions of the model, i.e. that the ratio between the foliage mass and the water conducting woody area is constant was tested using trees from very different climates. Apart from that, the mathematical model that links the different hypotheses together was used to simulate various aspects of tree and stand growth. The simulation results were compared with empirically observed trends.

The effect of some rather poorly known processes on the outcome of the simulations were examined. This was carried out in order to elucidate the role of these processes in growth and to suggest directions for future work, both theoretical and empirical, in the field.

3.2 Relationship between the water transporting wood and foliage

3.2.1 Linear foliage mass and sapwood area relationship and the balanced internal state

The internal state and the internal processes of the plant were defined in Chapter 2 as the internal concentration of substrates and compounds within the plant plus the processes by which they are transported between different structures and transformed into other readily reversible forms or into more permanent structures. A balanced internal state was assumed such that the in- and out-flows of substances to and from different biomass compartments match the material consumption in the same compartments so that the substrate concentrations remain stable.

A balanced internal state was also assumed to apply for water flows. As plants grow in volume, also the amount of accumulated water in them increases similarly as the amounts of carbon and the nutrients. Some of the water taken up is split into its components in photosynthesis. However, these two components form only a minor proportion of the fate of the water taken up by plants. The majority of water by far flows through plants from soil to atmosphere. At the same time, the flow also transports substances from roots to shoots. As mentioned in Chapter 2.1, the driving force for water flow is transpiration that is determined by the immediate environment of the leaves but also by the water availability in soil. Also, the review on the physiological role of the woody structure (Chapter 2.1.2.7) indicated that woody structure can be an important determinant of the flow of water in stem and branches.

The constant concentration of water in plants results when the amount of water entering and leaving plants is constant over any longer period of time. However, this condition is met at zero flows in the system. Since the photosynthetic production is necessarily associated with water loss, there must be water flow through plants if they are to survive. The structure of plants has an important role in conveying the pull of transpiration from leaves to the uptake of water by roots. Too small transport capacity would hinder photosynthetic production. It would not allow sufficient water uptake. This means that some of the available water would not be utilised. A large transport capacity would waste carbon resources. If water availability was restricted, large transport capacity would facilitate a rapid depletion of water resources from soil. This could be harmful later in the growing season. So, it could be assumed that there exists a balance between the amount of foliage and the water transporting structure in species adapted to certain conditions. The quantitative relationship of the above factors would then determine the range of conditions in which the species could thrive.

One could thus expect to find a rather constant relationship between the amount of foliage and water conducting capacity in stem in similar growing conditions and for the same species. The quantity of water that flows through any surface for a given time unit is surface area times flow velocity. The flow velocity in coniferous wood depends on the tracheid size distribution (e.g. Zimmermann 1983). The constant relationship between the cross-sectional area of wood that transports water and the foliage biomass above it assumes that the internal structure of wood would remain constant within the stem. It also assumes that a unit mass of needles would transpire a constant amount of water at different parts of the crown. The relationship remains unchanged also if these factors change as much relative to each other.

It is apparent from the literature review, that there is systematic variation in the woody fine structure affecting the water transport properties within trees. Also, environmental conditions can affect, e.g., the size of tracheids (see Chapter 2.1.2.7). However, the effect of the internal structure on water transport at the tree level is not so clear. Water flow is fast in large tracheids but they are simultaneously more vulnerable to cavitations (Carlquist 1988).

Water conducting measurements (e.g. Huber 1928; Zimmermann 1983; Ewers and Zimmermann 1984) and structural measurements (e.g. Whitehead 1978; Albrektsson 1984; Espinosa Bancalari et al. 1987; Keane and Weetman 1987; Long and Smith 1988) have demonstrated that the principle of constant ratio does not apply for all the trees growing in different conditions. However, there are also frequent observation of linear ratio between wood cross-sectional area and quantity of foliage, measured either as leaf area or biomass basis (e.g. Whitehead 1978; Kaufman and Troendle 1981; Long et al. 1981; Waring et al. 1982; Hari et al. 1986a).

Much of the work done on Scots pine has suggested that, at least at stand level, the ratio between foliage mass and sapwood area is quite constant (e.g. Whitehead 1978; Albrektsson 1984; Hari et al. 1986a). Hari et al. (1986a) measured similar values from two different stands growing at very different locations but in similar climatic conditions. However, the relationship could be different in trees adapted to conditions of different evapotranspiration and water availability. Let us assume that the degree of stomatal closure would be on average constant in all conditions. At higher average rate of evapotranspiration there would be either less foliage per sapwood cross-sectional area or higher flow velocity in wood than at lower rate. As opposite to constant degree of stomatal closure, Kaipiainen has reported that a unit mass of needles of Scots pine transpires constant amount of water in very different climatic conditions (Nikinmaa et al., manuscript). According to that, the canopy conductivity is smaller in conditions of high average rate of evapotranspiration than in those of low rate. This could be associated with smaller water transport capacity per unit foliage mass, respectively.

The outcome of the growth of Scots pine trees was measured in order to test the generality of the simplifying assumption that the cross-sectional area of sap-wood per needle mass remains constant. The measurements were carried out in different climatic conditions and the results were compared with the hypotheses presented.

3.2.2 Material and methods

Seven young Scots pine stands from different locations were analysed. There were two stands from Muddusniemi, Finnish Lapland (a and b) (69°N, 27°E), one stand from Hyytiälä, Central Finland (c) (62°N, 24°E), two stands from Siuntio, South Finland (d,e) (60°N, 24°E), one stand from near to Irkutsk, Siberia (f) (53°N, 103°E) and one stand from near Voronez, South Russia (g) (52°N, 40°E). In addition, the data measured at one stand from Petrosavodsk, East Karelia (62°N, 34°E) presented earlier by Hari et al. (1985) was included in the analyses.

The selected stands were either of local origin or had been established with routine methods and seed material used in forestry within the region. In each case, the canopy had closed recently. The measured stands were growing on medium fertile to poor soils, with the exception of Irkutsk stand (f) which grew on a fertile site. Voronez stand (g) differed from the rest in that it grew next to a pasture field. A sample plot of about 100 trees was limited at each stand, and the diameters and heights of the trees were measured. The sample plots were positioned so that their distance from open space or adjacent stand was at least twice the tree height.

Table 1. The main characteristics of the experimental stands.

Location	A y x	Height m x	 s	D1.3 cm x	 s	Hcr m x	 s	Dcb cm x	 s	Density n/ha	Gcb m^2/h a	Size sp m^2	N	sample plot
Voronez	16	7.5	1.9	7.6	3.1	4.3	0.6	5.6	2.3	6320	15.6	125	79	g
Irkutsk	24	6.7	1.3	7.2	3.0	2.6	0.4	6.3	2.6	4900	15.3	100	49	f
Siuntio 2	17	6.1	1.4	7.8	3.3	2.1	0.5	-		3400	-	300	102	e
Siuntio 1	15	4.9	1.4	7.3	2.7	0.9	0.4	-		1950	-	600	117	d
Hyytiälä*	22	9.4	1.6	11.6	1.6	5.2	0.6	7.3	2.1	2900	12.1	300	87	c
Muddusn.2	36	4.4	1.1	3.7	1.4	2.6	0.6	-		12200	-	100	122	b
Muddusn.	43	3.2	1.3	4.3	2.1	1.1	0.4	3.6	2.0	5333	5.4	150	80	a

D1.3 = diameter at breast height
Hcr = height of the crown base
Dcb = diameter at the crown base
Gcb = stand basal area at the crown base
Size sp = Size of the sample plot
*The Hyytiälä values with the exception of diameter at breast height were calculated from the sample trees.

Table 2. The general properties of the experimental trees in the different locations.

Location		Muddusn. (a)	Muddusn. (b)	Hyytiälä (c)	Siuntio (d)	Siuntio (e)	Irkutsk (f)	Voronez. (g)
N of trees		17	15	16	14	14	23	16
Dcb,cm	x	4.92	3.63	7.2	6.81	6.98	5.22	4.89
	s	2.12	1.47	2.1	3.07	2.62	2.85	1.75
Height,	x	4.17	4.7	11.6	5.14	6.32	6.40	7.63
tot.	s	1.21	1.08	1.6	1.15	1.65	1.87	1.03
Hcb,m	x	2.72	2.67	5.2	0.99	2.03	3.80	4.09
	s	0.94	0.62	0.6	0.47	0.53	1.51	0.92
Br/Wh*	x	3.2	2.0	4.7	6.07	5.52	5.3	5.9
Living* whorls	x	20.3	22.1	8.6	6.87	6.47	8.80	7.7
Age, y	x	38.4	36	22.0	15	17	22.5	16.0
	s	6.11	–	–	–	–	1.68	–

Dcb = diameter at the crown base, Hcb = height of the crown base
Br/Wh = number of branches per whorl, * the number of sample trees from which branches and whorls were counted was 3 in Muddusniemi (a) and 7 in Irkutsk. At the other places the values were counted from all trees

Table 1 presents the general properties of the experimental stands. The stands of Muddusniemi and Siuntio (a, b and d, e) had both dense and spaced growing densities. The Muddusniemi stands were just about to reach canopy closure, whereas the height of the tree crowns was already at dynamic phase in Hyytiälä and Voronez stands. The Muddusniemi and Voronez stands had double peaked size distribution, which is often associated with the high competition during the canopy closure (Ford 1975).

The sample trees were selected subjectively from the sample plots a, f and g from all the size classes with equal weight. The trees were selected randomly from the stands b, c, d and e. Equal number of trees was chosen from two different strata (trees bigger and smaller than the basal area medium tree) (b, d, e) or the sample of trees was chosen from all the trees of the sample plot (c). The number of trees measured per stand varied among 14 to 23. Table 2 presents the average characteristics of the sample trees.

The diameters of all the branches below the lowest living whorl of sub-branches and stem diameter below the crown base were measured. Also the diameters and heights below all the other living whorls of branches were measured from the stems with exception of one Muddusniemi stand (a). The diameter measurements were carried out at two perpendicular directions below bark. In branches the cross-section was perpendicular to the longitudinal axes of the branch and the diameter measurements were carried out at 45° angle between the horizontal and vertical planes of the cross-section. A whorl of branches was alive if there were at least 50% of the major branches still living, both in branches and in the stem.

The sample branches were selected using two methods. Fifteen to twenty branches of different size and position in the canopy were chosen subjectively from the subjectively selected trees. From the randomly selected trees, systematic sample was selected in two different ways. In stands b, d, and e, a sample branch was chosen each time the cumulative branch cross-sectional area surpassed one fifth of the total branch cross-sectional area. Thus, altogether five branches were selected. In the Hyytiälä stand, (c), every third branch of the crown entered the sample. The foliage of the sample branches was removed, dried (105° C, 24 h) and weighed.

The dynamics of the analysed ratio were tested in Hyytiälä and Voronez from one tree at both locations. The lengths of the newest shoots and the internodes not bearing needles just below the oldest internodes bearing needles were measured. A systematic sample of 20 and 28 shoots, respectively, was selected from the trees and the length of the shoot and the needle dry mass of the shoot measured. Also, the total diameters of the branches below the lowest living whorl of sub-branches and below each living whorl in the stem were measured from both trees as described earlier. In addition, the width of the newest tree ring was measured at four points at both ends of the diameter measurement axes.

The measurements were carried out either during the maximum foliage biomass after the cessation of foliage growth but before the onset of senescence (early august) (a, f, g) or during the rest period when the foliage was at the annual minimum in late autumn (end of October, c) or in early spring [end of April, beginning of May (d, e) and end of May, (b)].

3.2.3 Results

3.2.3.1 The foliage- wood regression

The regression between the foliage dry mass and the wood cross-sectional area was linear when measured during the maximum needle mass but the slope of the regression line varied between the different locations (see Figure 3). Southern conditions increased the slope (see Table 3). The ratios calculated from the Petrosavodsk data of Hari et al. (1985) were included.

The observed values varied more when the measurements were carried out during the minimum needle mass (see Figure 4). The ratio between the amount of needles and the wood cross-sectional area changed clearly as the age of the branches increased. The ratio seemed to decrease in southern Finland indicating that there was more wood cross-sectional area per foliage mass in older branches than in young ones. However, in old branches also the proportion of annually senescing needles from the total needle mass was bigger. The slight exponential nature of the observations from one of the Siuntio stands could result from the fact that the branches of the upper crown are among both the smallest and the biggest branches of the tree. In these branches the needle senescence represents only a minor proportion of the total needle mass. Branches of the intermediate size are mostly the once biggest branches which are now left to the shade crown and therefore have rather a big proportion of the total needle mass in dying needles.

The change in the needle mass and the associated tree ring area had a similar linear relationship to that of the total needle mas and the sapwood area. This suggests that the growth of the new tree ring area is connected to the change in the needle mass that there is above the point of observation (see Figure 5). The difference in the slope of the regression line between the trees was proportionally of a similar magnitude as the difference in the total mass - sapwood area measurements at the same locations. However, the same change in the needle mass seemed to imply smaller change in the tree ring area in the dynamic examination, especially in the Voronez stand. The big variation and the low number of stems in the dynamic examination naturally make the comparation difficult.

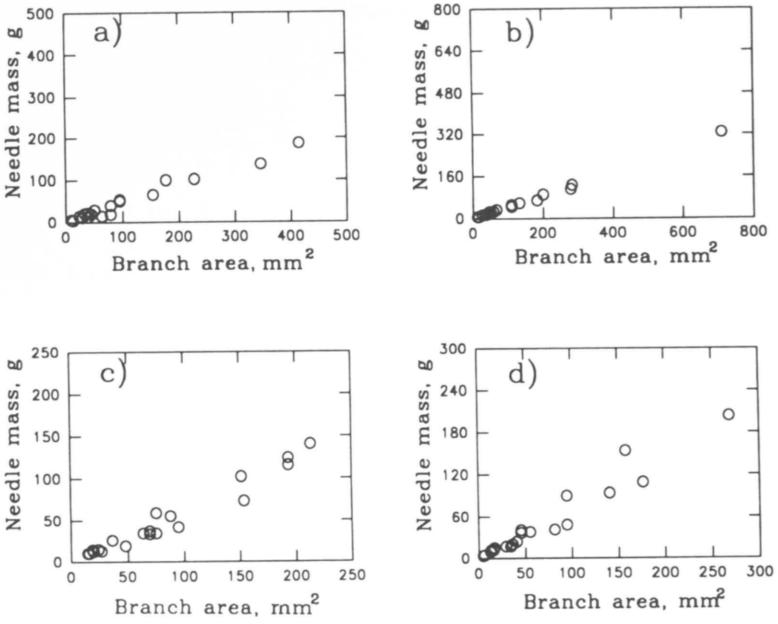

Figure 3. The relationship between the foliage mass and the branch cross-sectional area at the branch crown base measured during the maximum annual needlemass in a) Muddusniemi, b) Petrosavodsk, c) Irkutsk and d) Voronez. The data for Petrosavodsk are from Hari et al. (1985).

Table 3. The regression equations of the needle dry mass as a function of the branch cross-sectional area below the lowest living whorl of sub-branches.

Location	Gradient	Std.error	Conf.lim 5% risk	Intercept	R-squared
Voronez	0.751	0.045	0.66–0.84	–1.93	0.939
Irkutsk	0.622	0.03	0.56–0.68	–1.46	0.964
Petrosav.	0.452	0.007	0.44–0.47	–1.19	0.995
Muddusj.	0.435	0.019	0.40–0.47	1.78	0.966

The negative change of the tree ring area was associated with the decrease in needle mass. This could indicate that the needles of other whorls reuse the transport capacity of older tree rings that the needles of the whorl in question used previously. This is what the constancy of the ratio between the amount of foliage and the cross-sectional area of sapwood predicts (see Equations 12–14). This result and the differences observed when the foliage mass-sapwood area ratio was examined during maximum and minimum needle masses indicate that the growth of the newest tree ring seems to be associated with the needle mass change from maximum to maximum. This is in accordance with the approach used.

3.2.3.2 Regression between the cross-sectional area of branch and stem

The regression between the sum of branch cross-sectional area measured at branch crown base of living branches and the stem cross-sectional area measured at stem crown base was mostly linear but considerable variation existed between the stands (Figure 6). The variation did not depend on the measuring time or the sampling method

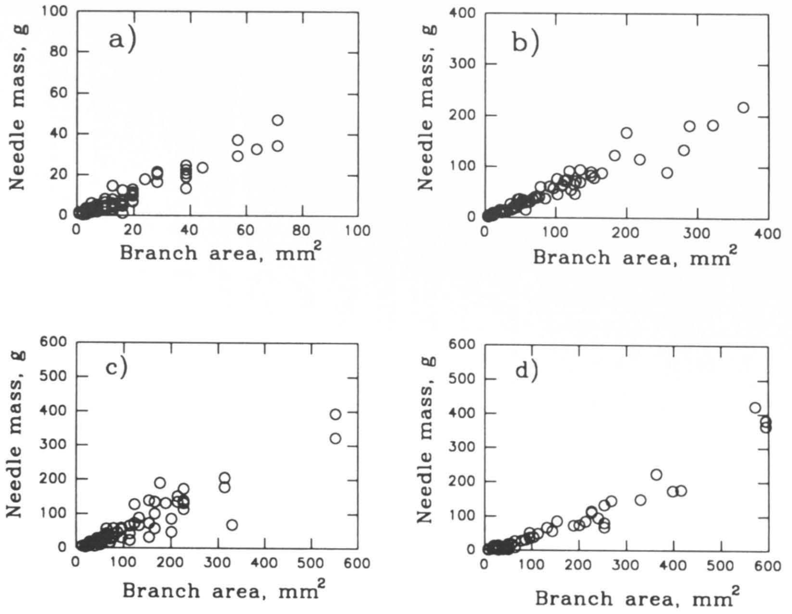

Figure 4. The relationship between the foliage mass and the branch cross-sectional area at the branch crown base measured during the minimum needle mass in a) Muddusniemi, b) Hyytiälä, c)Siuntio (d) and d) Siuntio (e)

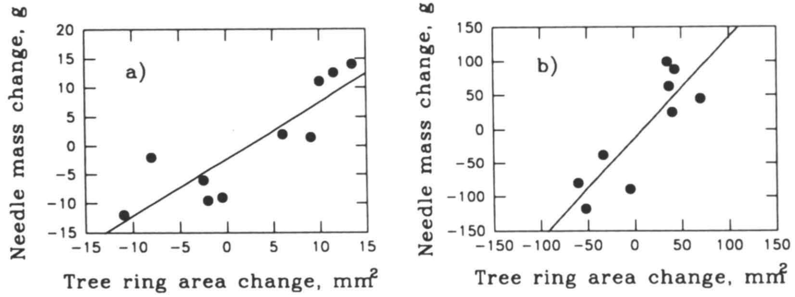

Figure 5. The relationship between the tree ring area change (the difference of the area of the newest tree ring above and below a whorl) and the needlemass change of the whorl in a) Hyytiälä and b) Voronez.

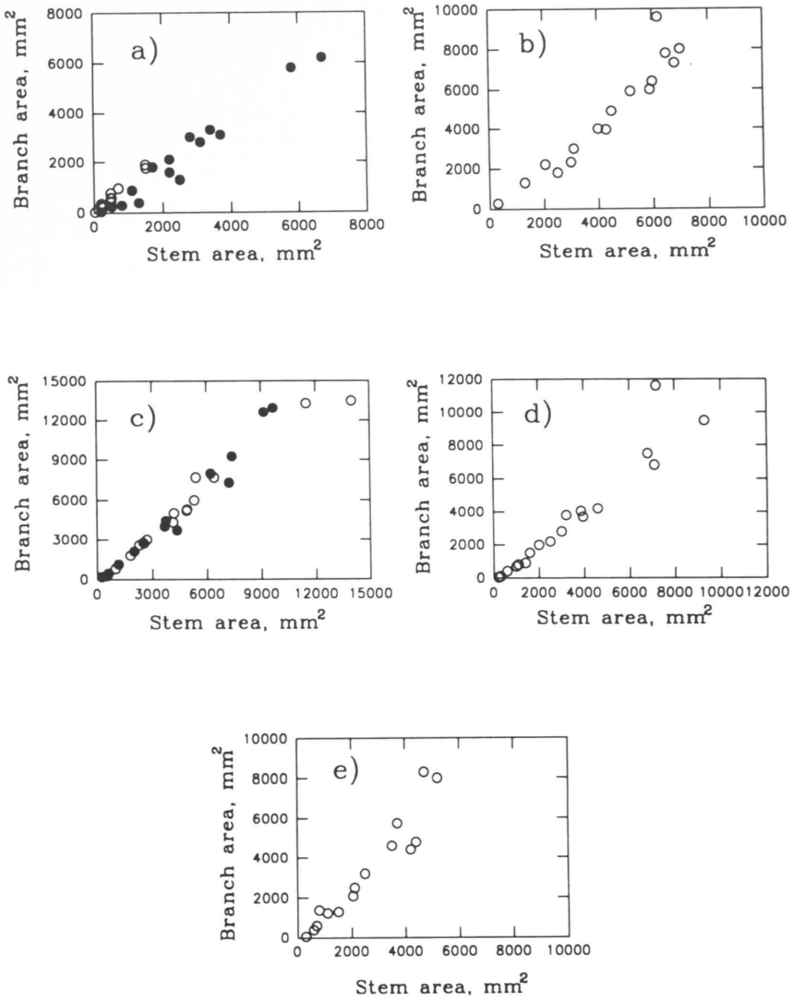

Figure 6. The relationship between the sum of branch cross-sectional area at the branch crown base and the stem cross-sectional area at the stem crown base in a) Muddusniemi (a and b are marked with different sign), b) Hyytiälä, c) Siuntio (d and e are marked with different sign), d) Irkutsk and e) Voronez.

but a north- to south gradient was apparent (Table 4). The values from measurements made in France by Berninger, (Department of Forest Ecology, University of Helsinki, unpublished) and Spain by Gracia, Retana and Gene (CREAF, Universtat Autónoma de Barcelona, unpublished) supported the observed trends. The same cross-sectional area supported more branches in the South than in the North. The biggest difference in the slope was about 100%.

Figure 7 presents the location of the study areas. The type of the regression seemed to change from north to south. It was linear in the North, but the bigger trees seemed to have more branch cross-sectional area per unit of stem cross-sectional area than smaller trees in the South (Figure

Table 4. The ratio between the crown branch cross-sectional area measured at the branch crown base and the stem area below the stem crown base. The French value is based on 14 sample trees from La Viale, near Montpelier at approx. 550 m above sea level measured by Berninger (unpublished). Spanish value is based on four trees measured from sample plot in Montesquie by Gracia et al. (unpublished).

Site	Intercept in mm^2 branch area	Regression coefficient mm^2 stem area	R^2
Muddusniemi 1	–19.23	0.78	0.96
Muddusniemi 2	–229.1	1.02	0.96
Petrosavodsk	91.5	1.02	0.94
Hyytiälä	–581.8	1.20	0.98
Siuntio	–52.3	1.16	0.95
Irkutsk	–280.3	1.05	0.99
Voronez	–723.5	1.57	0.92
La Viale	–589	1.53	0.93
Montesquie	–1269,13	1.81	0.99

6). Also the intercept of the regression line had generally bigger negative values in the South than in the North. The effect of the foliage attached to the stem was not taken into account in the stem area. It can be proportionally rather big in small trees. On the other hand, even within the same sample plot there where individuals which differed in appearance from the rest of the stand and had a totally different ratio between the observed variables from the rest of the stand (Figure 6, b and e).

The dimensions that are connected to mechanical stability of tree were also examined. The height -diameter ratio for trees in Muddusniemi sample plot (a) in Lapland was much smaller for trees than in Voronez (g) but there was also big difference in the stand density. The mortality of trees due to canopy closure had started in Voronez whereas the Muddusniemi stand was about to be closing. On the other hand, comparison of the diameter at the crown base of branches and their lengths between Siuntio and Muddusniemi did not give any significant differencies between the stands in this respect.

The ratio between foliage mass and the stem cross-sectional area did not change within the crown systematically in any of the northern stands but there was quite a clear pattern in Voronez. The amount of needles per cross-sectional area increased when going downwards in the crown until the lowest two to three whorls. There the ratio started to decrease again.

Figure 7. The locations of the experimental stands.

3.3 Simulated tree and stand growth

3.3.1 The bases of the simulations

The simulations of tree and stand growth had two main purposes. First the theoretical considerations presented in chapter 2 could only be tested if they were used to produce quantitative results that could be checked against observed trends of real world. Second the theoretical framework should connect various aspects of forest growth in a new way and describe or predict some new features of the functioning of the forest in order to be something more than just another way of describing the already rather well known general trends of tree and stand growth. For these reasons, the presented framework was used to investigate how varying some, still rather poorly known phenomena affected the outcome of the simulations.

The points investigated were the following: (1) How the outcome of the simulation is affected by the variation of the observed structural regularities. This approach was applied to simulate growth for different geographical conditions. (2) How growth differs when calculations assume a) average dimensions for the tree as in the model "crown" and b) optimal combination of shoot level growth as in the "branch" model. (3) How the outcome of simulations is influenced by connecting the heartwood formation to crown dynamics as the pipe model suggests (Shinozaki et al. 1964 a) and Kaipiainen and Hari (1985) have observed. (4) How a more detailed treatment of the nutrient balance of tree in which nutrients retranslocate from dying needles and roots compete for nutrients in similar fashion as the needles compete for light, affects the results of simulation.

The presented theoretical framework of forest growth describes the general patterns of the assumed interactions between the different components of trees and stands. The parametrization of the model actually quantifies these relationships and therefore it has strong influence on the simulation outcome. The parameter values used were generally taken from the literature. However, for some parameters no direct measurements were available. Their value was chosen to give as realistic outcome as possible of the feature whose relations the parameters were describing. The comparison criteria were mostly those from the Calluna-type forest of southern Finland. This kind of fitting was necessary for some of the "aggregation" functions of the model "crown" that Appendix 1 presents. Appendix 5 presents an example of the used parameter values and their sources, separately for both models, since their structure is different and thus they have different parameters.

The main interest was to study, how well the chosen approach could predict the general patterns in the forest growth and development. Therefore, no comprehensive study of the effect of all the poorly known parameter values on the simulation outcome was attempted. Only the values of those parameters that were studied separately were varied. The parameter sets that Appendix 5 presents are the basic set of values for both models. They are supposed to correspond to the conditions of growth zone of South Finland [Hyytiälä, (62°N, 24°E)] in the growth and yield tables (e.g. Ilvessalo 1920).

The photosynthetic parameter was an average value for a long time period using the available climate data from Hyytiälä and surroundings and the photosynthetic model made based on the field measurements (Korpilahti 1988). The respiration parameters were based on the same climatic data and the experimental results reviewed by Mohren (1987) and Schäfer et al. (1991). The nutrition parameters were averages from various stands (Mälkönen 1974). Most of the structural parameters were based on the measurements of one or two stands in the Hyytiälä region but also on the measurements made in similar stands in Russian Karelia (Hari et al. 1985).

3.3.2 Simulation of stand growth of Scots pine

The general features of the growth and development of Scots pine stands were the fast increase of the productive organs (i.e. needles and fine roots) in the beginning of the stand development followed by a more stable phase after the canopy closure. This was associated with a more gradual growth of stem and branch biomass. However, the closure of the canopy was reflected on the branch mass development. The transport root mass continued to increase for a longer time than the fine root and foliage masses but its culmination occurred earlier than that of the other conductive organs (Figure 8).

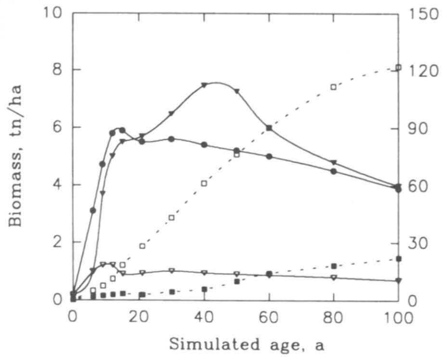

Figure 8. The simulated development of the needle mass (filled circles), the branch mass (filled boxes), stem mass (open boxes), transport root mass (filled triangles) and fine root mass (open triangles). The left scale is for needles, transport roots and fine roots and the right scale is for branches and stems.

The different simulated variables were comparable to the measured values. The foliage, stem and branch biomasses were of the same order of magnitude as the observed values in Southern Finland (e.g. Ilonen 1981, Ilvessalo 1920). The simulations for Hyytiälä gave about 11 kg needles for trees of the biggest size class at 100 years and an average branch length of 3.4 m. Those values were of a similar magnitude as the values reported by Hakkila (1972). He also reported that the branch mass of individual trees was 10 to 20% of the bole mass (diameter above 6 cm) in southern Finland when the crown ratio of trees is 40 to 60%. The simulated branch mass was 20% of the total stand stem mass in Hyytiälä. The development of height and crown base height also resembled the general trends observed (Figure 9, Ilvessalo 1920). Initially, the height growth seemed to be too fast, though. The height of the biggest size class of the simulations was compared with the average height of stands. This could have caused, at least partially, the differen-

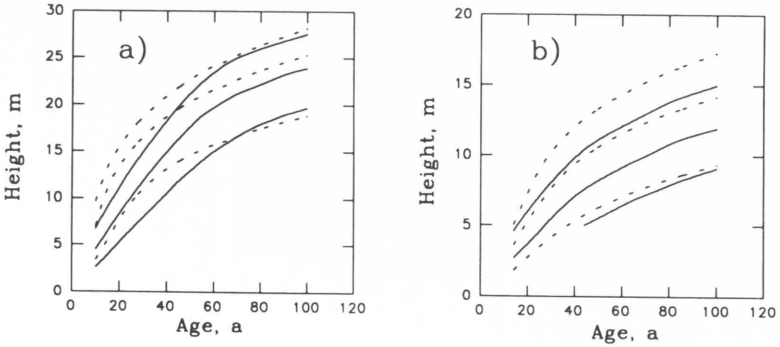

Figure 9. The simulated (dotted line) and observed (solid line) height growth for a) South Finland and b) Lapland. The observed values are from Ilvessalo (1920, 1970) .The site types of South Finland are Ct , Vt, Mt and OMt and the site types of Lapland are Clt, ErClt and EMt. The simulated values were obtained by varying the value of e_f^*(0.01, 0.0145, 0.0181, 0.02 in South Finland and 0.0073,0.0106 and 0.0146 in Lapland)

ces. Initially, the biggest size class corresponds to the dominant height. As the number of trees in the other size classes decreases, the values of the biggest size class correspond more and more to the average values of the stand.

The simulated development of the number of trees per hectare had qualitatively the same shape as in the growth and yield tables (Figure 10, Ilvessalo 1920). The model also seemed to produce a similar double-peaked size distribution as is observed in young stands after the canopy closure (e.g. Ford 1975). The used approach was also able to produce the difference in the stem wood production between the different site types just by changing the parameter value for nutrient uptake per unit mass of fine roots (Figure 11). This is in accordance with earlier findings with similar methodology (Mäkelä 1988). The allocation pattern of carbohydrates between different biomass compartments was very dynamic (see Figure 12) and qualitatively corresponded with the few estimations made on carbon allocation patterns (e.g. Ovington 1957; Albrektson and Valinger 1985; Mohren 1987; Reiners 1988).

3.3.3 *Geographic variation in the simulated stand development*

The use of the presented approach was developed to a more general study of growth in different climatic conditions. Also, it was studied how the earlier observed differences in the structural parameters affected the outcome of the simulations (see Chapter 3.2).

To approximate the changes in the growth of Scots Pine stand in different climatic conditions, a) the functional parameters describing the process rates were modified according to the length of the growing season at each location and b) the values of the parameters describing the dimensional regularities in the different parts of tree were varied based on the measurements performed in the different locations. The Hyytiälä values were the reference values for the parameters connected to photosynthetic production, respiration and nutrient uptake (P_0^*, r_{mn}, r_{mb}, r_{ms}, r_{mt}, r_{mf}, σ_n and e_r*). The values for other locations were adjusted by multiplying the Hyytiälä values with the relative length of the growing season at each location as compared with the length of the growing season in Hyytiälä. The structural parameters (β_{pw}, $\varepsilon_b\gamma_b, \varepsilon_s\gamma_s, \varepsilon_{tr}\gamma_{tr}$) were the measured values for the different locations (see Chapter 3.2). The wood density was not changed between the locations. It was assumed that the opposing trends of north-south gradient and the growth rate in the density of the trees would cancel out each other (Hakkila 1968; 1979).

Appendix 5 presents the parameter set and the parameter sources used for simulating the growth of the Hyytiälä stand. Table 5 presents the parameter values that vary from one location to another. The locations for the simulations were Muddusniemi in Lapland, (69° N, 27° E), Hyytiälä in Southern Finland, (62° N, 24° E) and Voronez, in South Russia, (52° N, 40° E). The different growing conditions were derived from weather data that was available for Murmansk, Jyväskylä, and Voronez and from the structural measurements carried out at Muddusniemi, Hyytiälä and Voronez. The length of the growing season was calculated from the daily average temperatures as the number of days which had average temperature continuously above 5°C (Hänninen, pers.comm.).

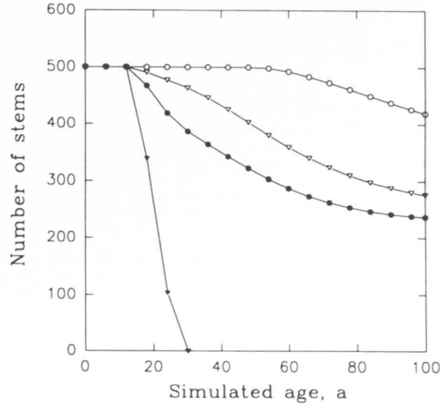

Figure 10. The simulated development of the number of stems in different size classes. Biggest size class (open circles), second biggest (closed circles), third biggest (open triangles) and the smallest size class (closed triangles).

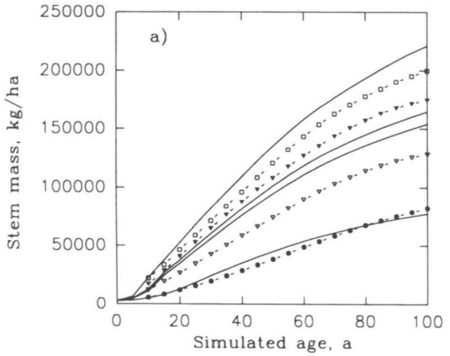

Figure 11. The simulated and observed stem mass development for South Finland. Simulated values are marked with solid line and the observed values are marked with dotted line. The observed values are from Ilvessalo (1920) from site types Ct , Vt, Mt and OMt. The simulated values were obtained by varying the value of e_f^*(0.01, 0.0145, 0.0181, 0.02)

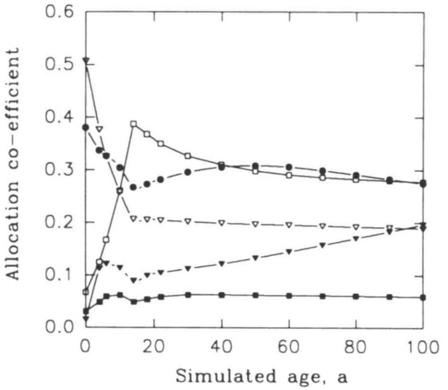

Figure 12. The simulated allocation of carbohydrates to needles (filled circles), branches (filled boxes), stem (open boxes), transport roots (filled triangles) and fine roots (open tringles).

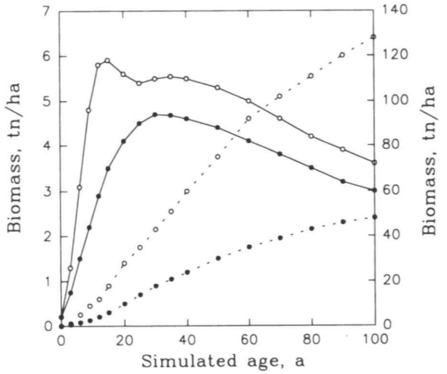

Figure 13. The simulated development of needle and stem masses in the South (open circles) and in the North (filled circles) Finland. The left scale is for needles and the right scale is for stems.

The same trends as observed for Hyytiälä simulations were present also in the other geographic locations. The main difference was that the initial development of the different biomass compartments was much faster in the South than in the North and that the levels reached were

Table 5. The parameters varied in the simulations and their values in different locations. See explanations in text and Appendix 5.

Parameter	Location		
	Muddusn	Hyytiälä	Voronez
P_0*	1.98	2.72	3.4
r_{mn}	0.13	0.18	0.225
r_{mb}	0.015	0.02	0.025
r_{ms}	0.015	0.02	0.025
r_{mtr}	0.015	0.02	0.025
r_{mf}	0.64	0.9	1.125
n_1	0	0.05	0.1
n_2	0.05	0.2	0.4
n_3	0.3	0.4	0.8
e_f*	0.0106	0.0145	0.018
β_{pw}	3	4	6
$\varepsilon_s \gamma_s$	0.98	0.78*	0.35
$\varepsilon_b \gamma_b$	0.89	0.89*	0.54
$\varepsilon_{tr} \gamma_{tr}$	0.45	0.45	0.64

* For determining the needle mass branch cross-sectional area ratio values from Hari et al. (1985) were used.

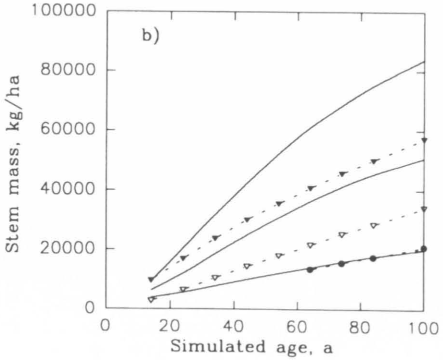

Figure 14. The simulated and observed stem mass development for North Finland. Simulated values are marked with solid line and observed values with dotted line. The observed values are from Ilvessalo (1970) from site types Ct , ErClt and EMt .The simulated values were obtained by varying the value of e_f^* (0.0073,0.0106 and 0.0146).

higher (Figures 8 and 13). The differences between Lapland and South Finland were mainly in the woody biomass compartment. The foliage mass developed faster in South Russia and remained at a higher level than in South Finland but the stem mass development was almost the same.

The approach predicted the changes of growth quite well within the climatic differences present in Finland (Figures 9, 11 and 14; Ilvessalo 1920, 1970). The initial height growth was somewhat faster than that observed in South Finland but otherwise the model could reproduce the growth and yield table differences of the different site types for Hyytiälä and for Lake Inari region as presented by the location Muddusniemi. The simulations for more southern conditions, as presented by the Voronez result, seemed to underestimate the yield of stem wood. Simulated results with very low cost of nutrient uptake (e_f* =0.1) produced comparable values for Hyytiälä with the observed values from the most fertile growing sites in the Southern Russian Karelia (625m^3 at 100 years as contrast to 700m^3 from the yield table; Kazimirov et al. 1984) whereas in similar combination for Voronez the simulation model gave 775m^3 at 100 years as compared with 1000m^3 from the yield table.

The effect of changing the structural parameters between sites according to the measurements was very clear. When the structural parameters of Hyytiälä were used for Voronez the simulations produced about 20% less foliage, about 80% more stem mass and about one third of the transport root mass compared with results when the structural parameters from Voronez were used.

3.3.4 *Crown dynamics*

Crown dynamics of trees are based on the pipe model and the functional balance considerations in the model "branch" (Chapter 2.2). This added a new component of dynamics on the stand development as compared to the results of the more aggregated model "crown". The changes of foliage biomass became more dramatic at the stage of canopy closure. This was also reflected more in the branch mass than in the model "crown". However, the development of the other biomass components was similar in both models (Figure 15). The dynamics of foliage biomass coincided with the observed values by Albrektsson (1980).

The simulated crown form dynamics behaved rather logically. A major proportion of the foliage biomass was in the lower parts of the crown when the trees were young or growing widely spaced. When the trees became older or were densely packed, the bulk of the foliage mass moved into the upper crown (Nikinmaa 1990). Simulated favourable nutrient conditions produced crowns in which foliage was concentrated more on the upper proportions. This agrees with the result of Brix (1981) from a fertilisation experiment (see Nikinmaa and Hari 1990). The pruning limit of the crowns was about the same in the trees belonging to the dominant tree classes but was clearly lower in the smallest size classes (Figure 16).

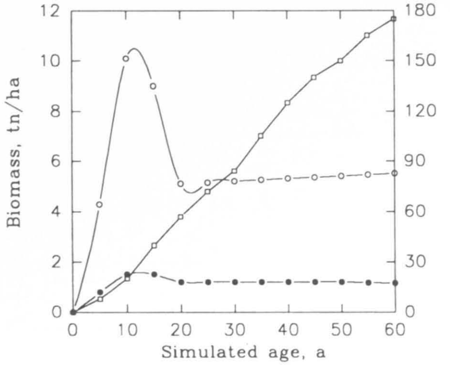

Figure 15. The simulated development of needle mass (open circles), stem mass (boxes) and fine root mass (filled circles). The left scale is for needles and fine roots and the right scale is for stems.

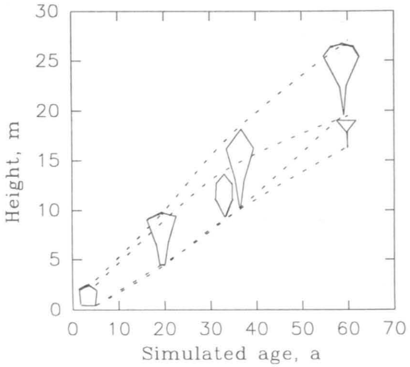

Figure 16. The simulated development of height, crown base height and the needle mass height distribution for trees of the biggest and the smallest size class. The crown width is proportional to the foliage biomass per height.

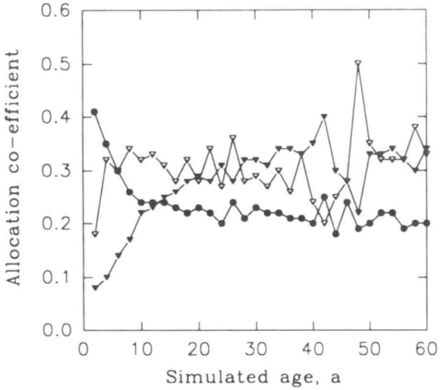

Figure 17. The simulated allocation of carbohydrates to needles (circles), stem (open triangles) and branches (filled triangles).

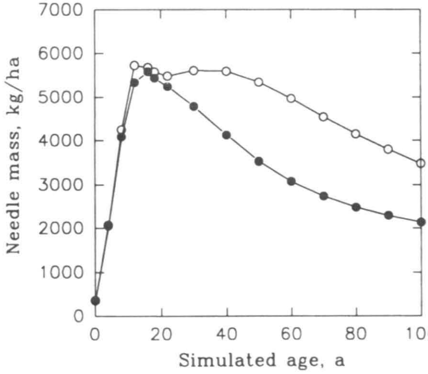

Figure 18. The simulated needle mass when 80% (filled circles) and 90% (open circles) of the senescing needles release transport structure to reuse.

The trend of the allocation of carbohydrates between different biomass compartments remained the same in the model "branch" as in the model "crown" but it became more dynamic, especially for foliage and stem wood (Figure 17). The fluctuations became bigger as the trees became bigger or when the trees became clearly dominated by others. The fact that the senescence of sapwood into heartwood depended on the changes of the pruning limit height caused some of the fluctuations as probably the oversimplified branching model. This shows in the allocation pattern; when more is allocated to the stem less goes to the branches. When the pruning limit moves higher, a smaller proportion of the dying needles releases transport structure in the stem for reuse. Thus the new needles require more new structure to support them in stem. From this it follows that a bigger proportion of the carbo-

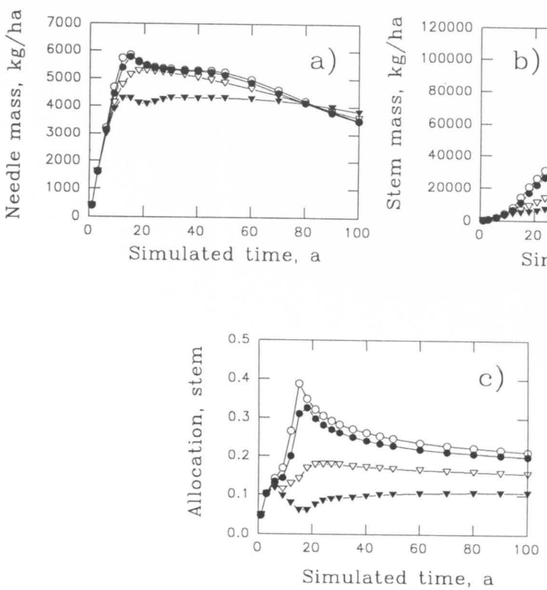

Figure 19. The sensitivity of simulated needle mass (a), stem mass (b) and allocation to stem (c) to the root competition parameter. Parameter values were: 0 (open circles), 0.0002 (filled circles), 0.0003 (open triangle), 0.0004 (filled triangle).

hydrates goes to the stem. In the opposite case, more needles and especially more branch wood is formed. Also, if the branching model produces too few new shoots at older ages, a high proportion of carbohydrates is allocated for their growth (see Equation 22). Thus, the average proportion of carbohydrates allocated to branches becomes bigger.

The practical realisation of the crown dynamics included parameters that were estimated using the fitting procedure described in Chapter 3.3.1. These were involved with aggregation from the more dynamic model "branch" to the model "crown". Also the calculation of sapwood release from senescing to functioning needles required simplification in the model "branch". Example of such simplifications is the parameter ξ of Equation (B8), which determines how different heights are weighed in the distribution of released transport structure for reuse. Also the maximal limit for the ratio between the growth of needles at given height and the growth of other structures required to support them was such a parameter (see Chapter 2.2.6). The simulations indicated that both models were quite sensitive for changes in these parameter values. If their values were such that too long crowns resulted in the early development of stand, the whole stand could collapse prematurely at about 60 years of age.

3.3.5 Turnover of sapwood to heartwood

The transport structure that served needles which died below the living crown in stem or in branches became heartwood in the models. Thus needles dying below the new living crown did not release transport structure to reuse in the models. The heartwood formation initiated in branches was approximated in the model "crown" by assuming that dying foliage would release to reuse only a certain proportion of the transport structure that has served them. The change of the pruning limit caused most of the heartwood formation in the early stand development whereas later on the heartwood formation in branches seemed to dominate.

The variation of the factors that affected the heartwood formation had a large effect on the outcome of the simulation (see Figure 18). The effect was very clear on foliage growth but rather small on woody growth. The factors affecting the pruning limit in the model "crown" affected the timing and the level of the peak needle mass mainly. The parameter for the formation of heartwood in branches affected mainly the needle mass of the later phases. In both cases there was remarkably little effect on the wood formation.

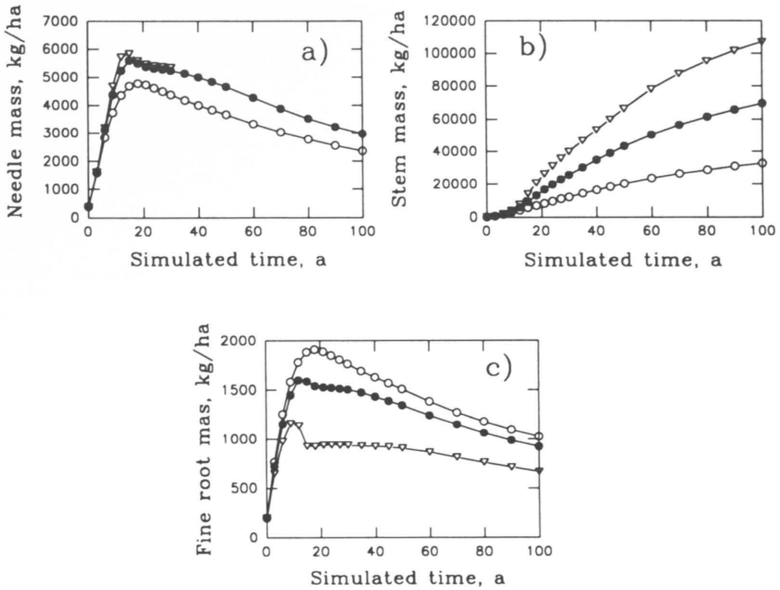

Figure 20. The sensitivity of the simulated a) needle mass, b) stem mass and c) fine root mass on the nutrient retranslocation from the senescing needles. Open circles represent no retranslocation, filled circles 35% retranslocation and triangles 70% retranslocation.

The effects of senescence are represented in Equation (18) in Chapter 2.2 by S_n and l_s. These show that the changes in senescence rates affect the growth of needles, G_n, and, consequently, growth of other biomass compartments, G_b, G_{st}, G_{tr} and G_f through Equations (11) and (15)–(17). The simulations demonstrate that small changes in the rate of heartwood formation change the allocation so that although the foliage biomass is much affected, the changes in woody mass can be quite small.

3.3.6 Effect of nutrients on stand growth

The availability of nutrients per unit mass of carbon used for fine roots affects the stand development as shown in Chapters 3.3.2 and 3.3.3. The model was very sensitive to the parameter for nutrient uptake rate, (e_f^*), at the range of values that produced a comparable stand development to the growth and yield tables. Especially at the lower range of values, a 40% increase in the parameter (from 0.007 to 0.01) caused a twofold increase in the allocation of carbon to stem whereas a change from 0.014 to 0.018 changed the allocation only by about 20%. However, no root interference was assumed in the simulation results of Chapters 3.3.2 and 3.3.3.

The effect of root competition on stand development was studied by changing the slope parameter, k_f, of Equation (A13) in Appendix 1. The higher the parameter value, the steeper was the effect of the fine root biomass on the root specific nutrient uptake rate. As can be seen from Figure 19, the effect on the biomass compartments and distribution of produced carbohydrates is clear. An increase from 0 to 0.0003 (fine root biomass in kg/ha) caused only small changes, but as the value increased from 0.0003 to 0.0005 a clear change in the allocation pattern took place. At the highest value the system oscillated before a stable development followed. It is interesting to note that the higher root interaction

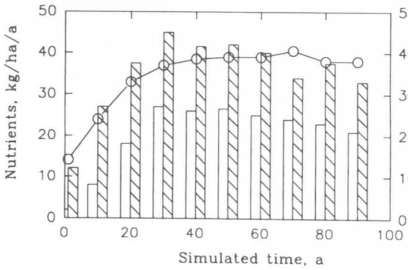

Figure 21. The development of internal nutrient circulation. Open bars present the simulated amount of internally circulated nutrients, hatched bars present the simulated annual nutrient uptake from the soil and the line gives the proportion of internal circulation from the total demand.

seemed to level off the initial hump in the needle mass development observed in Chapters 3.3.2 and 3.3.4.

The effect of retranslocation of the nutrients was studied by varying the proportion of the nutrients that are retranslocated from the senescing needles from 70% [lower range of the values reported by Helmisaari (1990) for nitrogen retranslocation] to 0%. Figure 20 presents the effect of such variation. The effect was strongest on the fine root and stem mass whereas the foliage mass was less affected. Carbon allocation between the different parts of tree was affected in a similar fashion as when the nutrient uptake parameter was varied. This is natural, since both terms describe the nutrient acquisition for the remaining and new structures. However, in contrast to what happens when the uptake rate parameter is changed, changing the retranslocation parameter does not affect the timing of the minimum or maximum allocation and causes a bigger change in the proportion allocated to fine roots.

Figure 21 presents the importance of internal nutrient cycling. Nambiar (1985) and Helmisaari (1990) point out that the retranslocated nutrients are a major nutrient source for new growth. Helmisaari (1990) claims that the significance of retranslocation depends on the phase of stand development. Simulation results suggest that the proportion increases until the maximum needle mass is attained. After that, the proportion of internally circulated nutrients stabilises to about 40% of the total nutrient requirement (see Figure 21). This falls into the lower range of the values estimated by Helmisaari (1990).

4 Discussion

4.1 The bases for the evaluation of the used approach

The objectives of this work were to develop and analyse a theoretical framework for the growth of Scots pines and to test the applicability of some key assumptions of the theory. Tuomivaara et al. (manuscript) suggest that there are certain critical aspects of theories that should be evaluated when analysing their validity. The theory should be consistent in itself and with other relevant theories that, for example, are operating at different hierarchy levels. The theory should be able to reproduce known or problematic facts about the research object. The theory should be independently testable, i.e. it should be able to produce some known or new results that were not exploited in the original construction of the theory. It should also consist of coherent and compact set of postulates, from which it is possible to derive many variables and correct consequences.

Unfortunately, the basic theoretical assumptions cannot be tested directly. Many additional assumptions are required before the concepts can be formulated to produce quantitative estimations that can be compared with real world observations. In this case, the basic theoretical framework for tree growth is presented in Figure 1 and in Chapter 2.1.1. There the role of growth in the spatially and temporally hierarchical system was rather well defined. However, many additional assumptions presented in Chapter 2.2 and Appendices were needed before simulation results could be produced which could be compared with observations.

Good correspondence of the simulation results with the observations gives support on the validity of all the assumptions made at different levels. When the model produces false results, it is more difficult to estimate at which level the error occurs. Therefore, the evaluation of the validity of the concepts should be done in steps: the first step should independently look at the validity of the components of the theory and the second one test how they are linked together (Sharpe and Rykiel 1991).

Testing of theory and thus process based models is complicated by the fact that it is not evident which is a good correspondence. The criteria by which a work is evaluated should change according to the objectives of the modelling (Sharpe 1990). In forestry, people are often satisfied with a descriptive statistical model if it describes the data to which it has been fitted with only a small error. However, it does not necessarily add any bit of our understanding on the phenomena (Sharpe 1990). At the same time, process based models are rejected, since they produce results with much larger error, even if they could add to our understanding on the functioning of a complex system. Bossel (1991) argues that one should evaluate the process based models using the criteria of behavioural validity, i.e. how well they can reproduce known patterns of the forest growth and development.

4.2 Analysing the theoretical framework

Growth and senescence are typically processes that depend on various factors. Dynamic models offer a valuable tool for their analyses, especially if we redefine prediction as organised thinking about the possible, as suggested by de Wit and Penning de Vries (1985). The process-based stand growth analyses frequently use the material balance framework. The state variable approach is a practical tool in such analyses (e.g. Thornley 1981; de Wit and Penning de Vries 1983).

The selection of the hierarchy level is an important decision when making the theoretical framework operational. Models with objectives of explaining are bridges between levels of organisation (de Wit 1982). Therefore the purpose of model used defines at which hierarchy level the model is operating (Bossel 1991). de Wit and Penning de Vries (1985) claim that models attempting to explain population level phenomena by molecular level functions serve no purpose. As Levin (1988) says:"...overly detailed and reductionist models of populations and systems obscure any pattern by introducing irrelevant detail...". A detailed description of tree level processes (e.g. Mohren 1987, Bossel and Schäfer 1989) or even processes at a lower level of hierarchy such as branch (e.g. Ford and Kiester 1990) is necessary if one wants to study the changes in tree functions. On the other hand, a description of only a few main processes may suffice when estimating long-term changes in the stand growth that are mainly caused by the stand development (e.g. Bossel 1991, Sievänen 1992).

This work concentrated on the description of growth processes. The short review on the main processes transporting and transforming material between tree and its surroundings indicated that the actual material exchange processes between the plant and its surroundings are relatively well known if compared to the internal processes that consume these materials in formation of the biochemical system and the permanent structure of trees (see Chapter 2.1).

A hierarchical system was outlined where momentary material exchange at a single exchange site depended on the environmental condition of the site outside the vegetative layer, the internal state of the biochemical system of the plant, the structure of the plant and other plants that determined the environmental condition at the exchange site and the genetic structure of the plant (Figure 1). The flows of various exchange processes over a period of time determined the internal state of the biochemical system and the internal state of the system determined the material consumption for growth. In that the outlined system resembles the idea of the growth-cycle concept introduced by Sharpe (see Sharpe and Rykiel 1991).

The outcome of the regulation of the internal processes was described with an assumption of balanced internal state. The functions of the internal communication system are problematic to describe with the state variable approach (e.g. de Wit and Penning de Vries 1983). These problems can be avoided by assuming certain functioning properties for the system. It is assumed that a steady state between the resource intake and the resource utilisation on growth is maintained at a tree level within the response rate of the different processes (e.g. Thornley 1972). Mäkelä and Sievänen (1987) suggest that a constant ratio between carbon and nutrients, i.e. resources taken principally by foliage and fine roots, could serve as a simplification of the principle, if the utilisation of substrates can not compensate for each other.

The traditional model of functional balance

(Davidson 1969) was changed to better correspond with long lived trees that have clearly different biomass compartments with different nutrient demands (e.g. Mälkönen 1974) and that can obtain a considerable amount of their annual nutrient requirement of growth through internal circulation (Helmisaari 1990). The present model was written as a carbon balance model, as is the majority of the process-based stand growth models (e.g. Hari et al. 1982, McMurtrie and Wolf 1983, Mohren 1987, Ludlow et al. 1990). However, it was simultaneously required that the nutrient balance of trees would hold (see Chapter 2.2). Therefore, similar equations as those written in carbon terms could be written at nutrient basis. In that respect, the model resembles the nutrient productivity approach of Ågren (1985). However, the actual balance equations are different in the two approaches.

It is assumed that the growth of a biomass compartment depends linearly on the nutrients allocated to that. Equation (11) shows that the root to shoot ratio depend inversely on the nutrient uptake per unit mass fine roots. The experimental results of Ingestad (1979) have demonstrated a linear relationship between the internal nutrient concentration and the relative growth rate of tree seedlings under steady state-nutrition. According to those results, the conversion efficiency of nutrients to structure, ω_N, would not be constant. The results of, e.g., McDonald et al. (1991) show that the concentration depends on the availability of other resources. If we allow the conversion efficiency to vary, the presented approach produces root to shoot ratio that is a Michaelis-Menten type function with respect of the conversion efficiency. Then it is assumed that the conversion efficiencies of nutrients to structure of the different biomass compartments are proportional to each other,

The conversion efficiency in the presented approach is the same as resource utilisation for growth. It could be replaced with a resource utilisation function, which describes the structural growth per unit of nutrients as a function of, e.g., uptake efficiencies. Also, an optimal growth problem could be formulated with respect of nutrient utilisation. These considerations would allow for variation in the nutrient concentration of the tissue. However, the equations of Chapter 2.2 demonstrate that the use of more complicated relationships than the applied linear ones can result into rather cumbersome solutions. In natural conditions, the nutrient concentrations seem to remain stable in certain soil conditions. Different levels result, e.g., as a response to fertilisation (e.g. Tamm 1989). Thus, the present approach modified so that the conversion efficiency depends on the soil condition, could be an accurate enough method, considering the general hierarchy level of the model. The strong influence that the rather poorly known internal circulation of nutrients has on the total nutrient balance of trees emphasises further this point.

The literature review also demonstrated that a close connection seems to exist between the growth of foliage and the woody tissue although the control mechanisms bringing this about are not yet fully understood. This close connection reflects the frequent observations of the constant ratios between the sapwood area and foliage mass or area. The constant ratio was assumed to describe the outcome of the balanced internal state as regards to the growth of the woody part of the tree.

General principles that can be justified by empirical results or evolutionary considerations were used to describe some poorly known control mechanisms to analyse tree and stand growth. The teleonomic arguments in models that analyse complex systems, such as forest stands, have value, although they have been criticised (e.g. Thornley 1991). The models using teleological arguments can be used for searching the boundaries set by a higher level requirement to a lower level phenomenon (Thornley and Johnson 1990, Sharpe and Rykiel 1991, Givnish 1985). Experimentally rather often observed growth patterns, such as the functional balance between foliage and roots (e.g. Brouwer 1962) and pipe model between foliage and wood (Shinozaki 1964a) can be used for processes, which are still relatively poorly known. Especially the control of resource partitioning seems to be such process (Nikinmaa 1992). The use of the guiding principle when modelling this process can give new insight, e.g., on the stand level growth.

The cost-benefit analyses, and the optimality principle on the other hand can point out the relative importance of the different structural adaptations or acclimation and thus increase our understanding of tree functions (e.g. Givnish 1985). As Küppers (1989) points out, different architectural patterns imply a different resource acquisition but also a different cost of acquiring them in terms of resources. Changes of resource ratios should have an effect on the different vegetation and succession patterns. The resource ratios should affect the cost-benefit relationships of different plants and plant forms that are not all adapted to the same resource availability (e.g. Schulze and Chapin 1987). Principally, the presented approach could be applied for this kind of analyses.

4.3 Testing the assumption of a constant ratio between the water transporting wood and the water transpiring foliage

The main operational assumptions of the model were those that describe the balanced internal state, i.e., a constant nutrient concentration in the different tissues and a constant ratio between the foliage and sapwood cross-sectional area. Within the theoretical framework, the first described the result of the regulation of the resource acquisition and utilisation and the second described the development of sufficient transport capacity to allow for the maintenance of the balanced internal state. As already pointed out, rather much work has been done on testing the basis of the first main assumption (e.g. Mäkelä and Sievänen 1987). For these reasons, the main emphasis of the independent testing of the key operational hypothesis of the theoretical framework was laid on the second assumption.

The results of the measurements supported the hypothesis at stand level. The relationship between the foliage mass of a branch and the cross-sectional area at the crown base of the branch was linear within stands. Also the relationship between the sum of the cross-sectional areas of branches measured at the same place and the stem cross-sectional area at the crown base was linear. On the other hand, the dynamic measurements, i.e. estimations of change of the needle mass and the change of tree ring area gave a linear relationship that should follow if the hypothesis is correct. The slopes of the dynamic estimations were slightly higher than those of the static examination but the material measured did not allow to estimate if the difference is significant. However, the relationship between the change in the foliage quantity and in the tree ring area is according to the hypothesis. It follows if the static "pipe model" is made dynamic (see Chapter 2.2.3, Equations 12–14).

The water transport velocity per unit amount of supplied leaves can be very different in different parts of crown (Huber 1928). The water transport velocity within the conductive cells depends strongly on the lumen size (e.g. Zimmermann 1983). There are clear and systematic trends in the tracheid size distribution in stems of conifers. They can be observed in the same tree ring from the top downwards and between tree rings at the same height from the pith outwards (see Chapter 2.1.2.7). Vysotskaya et al. (1985) report tracheid size variation depending on the site conditions. In spite of these observations, there are the apparently contrasting results of constant linear relationship between the crown foliage biomass or area and the sapwood cross-sectional area at the crown base within a stand (e.g. Whitehead 1978, Kaufman and Troendle 1981, Waring et al. 1982, Hari et al. 1986a). A similar relationship was also observed in this study with the possible exception of the most southern stand.

The regression lines for the different locations were clearly different in southern and northern stands. Trees of the southern conditions could support about three times the foliage of those of Lapland with the same cross-sectional area. Kaipiainen (Nikinmaa et al., manuscript) has observed that the stand level transpiration per needle mass is approximately constant in different conditions. This means that the annual water flow per unit cross-sectional area would be about three folds in trees of southern conditions compared to those of Lapland. On the other hand, the growing period is longer in the South and the potential evapotranspiration is higher there than in the North. This and the constant water flow per unit mass of needles suggests that the average canopy conductivity is lower in the South than in the North. It can be that the smaller amount of sapwood cross-sectional area observed per unit mass of needles plays a role in bringing that about.

It seems that, either water permeability of wood changes strongly when going to more favourable growing conditions or the woody structure plays a role in the water balance of a tree. Pothier et al. (1989) have demonstrated that the sapwood permeability changes as a function of the site quality and it is connected to the changes in tracheid structure. At young ages, the permeability correlated with the lumen diameter. The findings are supported by the results of Vysotskaya et al. (1985). Coyea and Margolis (manuscript), on the other hand, found that the relationship between the leaf area and sapwood area in balsam fir (*Abies balsamea* (L.) Mill.) was positively correlated with sapwood permeability. Thus, similar permeability changes could have taken place in the trees of these studies.

The control of the woody growth seems to bring about linear regression between the amount of foliage and the sapwood cross-sectional area at the crown base. The size distribution of the water conducting vessels or tracheids would thus need to be similar there at stand level. However, there is evidence from many species that the regression does not remain constant at other heights (Huber 1928, Waring et al. 1982, Tyree et al. 1987). We found (Ärölä and Nikinmaa, (unpublished result)) that the sapwood cross-sectional area at 1.3 meters was about double to that at the crown base. The ratio between early and late-wood starts to decrease below crown or lower parts of the living crown (Larson 1969, Hari, Department of Forest Ecology, University of Helsinki, unpublished). This could explain why the ratio of the cross-sectional areas between branches and stems started to decline in the lower parts of the crown in Voronez and is so different at the breast height compared to crown base. However, the same reason could not explain the changes in north- south gradient. There seems to be proportionally more late wood in the southern trees than in the northern trees of the same size (Mikola 1950).

Zimmermann (1983) introduced a model of hydraulic architecture of trees. It suggests that water conductivity is lower at distal points of a tree than in the main stem. This hypothesis coincides quite well with the general observations that the tracheid size changes within the tree in height direction and also at given height laterally (Sanio 1872, Helander 1933, Bailey 1958, Dinwoodie 1961, Burley and Miller 1982). The observations of this study may support that idea in the southernmost conditions. There one could observe increase in the ratio between branch area per unit stem area, which could reflect changes in conductivity when moving downward in the upper parts of the crown. Even there it was not very clear.

Tyree and Sperry (1989) suggest that the negative effects of drought and their limitation only to the most distal branches are not so important for trees living in the more northern climates. It is more crucial to be able to avoid xylem dysfunction due to winter embolism. This would mean that trees growing in cold climates would need to have structures that either avoid winter embolism or facilitate fast restoration of any damaged parts in their water conducting pathway. Cold temperatures in the winter are affecting water in wood almost equally at any point. From the above, it could follow that the fine structure of wood could be more or less independent of the position in the water transport system in the North as contrast to the South. Thus, the pipe model considerations could hold better in the North than in the South.

The mechanical stress caused by snow loading during winter has a clear gradient in North South direction. Various people have explained the stem form quite successfully on the basis of mechanical considerations (review by Assmann 1970, Ylinen 1952). The same considerations can be used to describe the structure of the branches (e.g. King and Loucks 1978, Cannell et al. 1988). In this study no clear trend could be detected that would have indicated geographical difference in the mechanical stability. It must be said, though, that the measurements were not designed to study that kind of effects.

A more mechanistic theory of the growth of trees is based on the source-sink considerations (see Chapter 2.1). According to these studies the sink strength of the growing meristems determines where the flow of photosynthetic products is going. The new foliage seems to be a strong carbon sink and draws photosynthates from nearby sources (e.g. Dickson and Iserbrands 1991). Favourable growing conditions can facilitate fast foliage growth. Thus a bigger portion of the carbon supply of the tree is drawn to the growth of new foliage and less is left for the stem. However, good conditions facilitate high total foliage giving also bigger stem growth in absolute terms. These considerations could explain the observed pattern of increasing ratio between foliage and stem cross-sectional area when going from North to South and why the ratio seems to increase in the southern stand as a function of tree size. Satoo (1956 1958, 1959, cited by Kozlowski 1971b) and Long and Smith (1988) observed a similar pattern with other species.

The used assumption appears to be an applicable tool in describing the control mechanisms bringing about wood and foliage growth of Scots pine, especially in the present conditions in Finland where the species is growing. In these conditions there are two aspects that need to be modified and analysed further. There seems to be tree-to-tree genetic variation that brings about different foliage/wood relationships. In Hyytiälä and Irkutsk there were outlying trees that had clearly differing values for the observed relationship and which differed in appearance, especially in Hyytiälä, from the rest of the stand. This may have a strong effect on the allocation of carbohydrates, as the simulations of the chapter 3.3.3 demonstrated. Also the dynamics of the development of different individuals can be affected. The so called "wolf trees" could be examples of that. Their consideration in the simulations could bring in a new component of dynamics in the analysis of stand development. The other aspect to consider in the future is the tracheid size distribution that can be observed along the ontogenetic development of the meristems. That can be done within the present model structure by varying the coefficient of proportionality between sapwood area and needle mass, ε, according to the height and age of the stem at that height.

It is more difficult to consider the changes of the coefficients at the same corresponding height that was observed in trees of different sizes in the southern stand. The consideration of the differences observed between stands is also difficult. However, this becomes necessary if the models are wished to be used in the conditions of changing climatic conditions. It is not clear if the observed changes are phenotypic of if they are due to the genetic code of the trees. The experimental stands were rather centrally situated in the regions of Svoboda´s taxonomic subdivision of the Scots pine of the European area (Giertych and Matyas 1991). Thus, the stands should have had rather different genetic compositions. Also, one would not have expected linear ratios within stands if the ratio between the foliage and the sapwood area depended on the growth rate, i.e. was a phenotypic feature. On the other hand, there was clear non-linearity in the measured values in the Voronez stand.

It must be clarified, to what degree the observed change is phenotypic and how strongly it is genetically controlled. The interaction of auxin, cytokinins and gibberellins controls the coupling of the foliage and woody growth. Thus, the growth processes are very closely tied to the annual rhythm of the trees (e.g. Larson 1969) which is under strong genetic control (e.g. Koski and Sievänen 1985). Therefore, the annual rhythm of trees belonging to different provenances determines quite strongly their growth. Because of this it is possible that major changes in foliage-wood ratios would not take place although climate would change. In fact, the observation that the ratio is less sensitive to the tree size in the North than in the South could indicate a stronger annual rhythm effect.

A general description of foliage wood ratios would require considering both the internal structure of the wood and its quantity in relation to the functioning and quantity of foliage. General lines to improve our knowledge in these respects would be to examine the quantity and functional quality of wood and the relationship it has to the amount of foliage and its functions in different conditions. In addition, the control processes between foliage and woody growth need to be studied at mechanistic level. According to Tyree and Sperry (1989), the model simulations have demonstrated that stomatal regulation and xylem physiology must evolve as an integrated unit in order to prevent catastrophic dysfunction. They conclude that trees must evolve mechanisms to keep an appropriate balance for carbon allocation between leaves, which increase evaporative demand, and stems, which supply the demand for water evaporated from leaves.

4.4 Evaluation of the approach

Evaluation of the approach requires testing of its components and the whole, i.e. how well the different composite principles are joined together within the theoretical framework. The main assumptions of the models used were those connected with the internal balanced internal state, i.e. constant concentration of different substances and the constant structural relationships. Previously the basic assumptions of the approach were dealt with. It was concluded that they can be used as an approximation when the analysis of growth is developed from biological principles, although they do not correspond exactly with the real world situation in every condition.

There were various other assumptions that were necessary in order to formulate the approach mathematically. Some of them followed from the principle of balanced internal state. Since it was assumed that the internal states remained the same, the uptake processes could be described with the variation in the external conditions. Some other assumptions used were basically simplifications of the real world, either because their importance on the outcome of the simulation was small in comparison with problems in their realistic description or because too little was known on the control processes involved. For example, it was assumed that only the light regime in the canopy would change so strongly that it needed to be considered in the analysis and that the wood density is a constant.

The additional assumptions were not tested separately, as the key assumptions, partially because at the moment that would have been either impossible or at least very laborious and was outside the scope of this work. The values used were based either on literature or field observations, mainly in the Hyytiälä region. However, the validity of the assumptions was studied by estimating how big an effect they had on the outcome of the simulation. The critical ones of these additional assumptions were introduced as hypotheses to improve the used theoretical framework. This gave some of those attributes that Tuomivaara et al. (manuscript) have identified for a good theory (see Chapter 4.1).

The general features of the growth and development of Scots pine stands were the fast increase in the productive organs in the beginning of the stand development followed by a more stable phase and a continuous and rather stable growth of stem biomass. This result is a direct consequence of combining the effects of light extinction and the pipe-model partitioning pattern (cf. Mäkelä 1990b). Qualitatively this pattern corresponds quite well with the observations (see Chapter 3.3.2). Using a realistic combination of parameter values, the observed patterns are similar to those reported in the growth and yield tables. These results give support to the presented approach.

Interesting result of the approach is that the variation of the foliage mass that produce a large difference in the growth of stem-wood growth is quite moderate. For example in Figures 19 and 20, about 20% smaller foliage mass produced about 70% smaller stem mass. The approach gives thus the same result as the so called priority principle (Waring 1987). When the resource availability is low, the resources are primarily used for the growth of uptaking organs. However, as the resource availability increases, a major proportion of the resources goes to growth of stem and other supportive organs.

As such, these results have also a direct influence on other fields of forest research. Allocation seems to be strongly connected to the size of a tree. This has consequences on the studies in which the genetic variability of allocation is studied. If there is a strong stochastic variation in the size of the trees due to variation in site conditions or in the establishment of the experiment, then this phenotypic trend might obscure the genetic differences.

The yield differences between different locations within the climatic conditions presently observed in Finland could be described by modifying the material exchange rates according to the length of the relative growing season of the location and by changing the structural parameters according to the local measurements. However, the same approach was not as successful in more southern conditions.

It was assumed that the growth processes match the resource uptake at annual basis and that the internal concentration of materials remains stable (see Chapter 2.2.1). However, the balance between the processes can change, when moving to very different environmental conditions, as the results over the structural regularities would suggest. Thus, both the internal concentrations of materials and the exchange processes could vary, since the latter depend on the former (see Chapter 2.1).

There was not enough data to estimate all the necessary parameters of the model for the different conditions. Still, surprisingly good fit with the observed could be obtained. However, there are additional calculations that would be necessary to produce the required parameter values even if the same data as from Hyytiälä was available from all places. For example, where the water availability limits the photosynthetic production one would minimally need to estimate the potential annual photosynthetic production as a function of the foliage mass of the stand and the water retention capacity of the soil. Similarly, the very basic way of describing the stand light conditions would need to be improved, e.g., according to the lines given by Kuuluvainen and Pukkala (1989). Also the effects of canopy on the transpiration, and in this way to photosynthesis, become more important in the southern conditions.

The generalisation of the model to a wider range of conditions requires additional work. The used approach offers possibilities for this provided that additional information is obtained on, e.g., the acclimation/adaptation of photosynthetic and respiration rates to temperature (see review by Skre 1991) and the variation of the structural regularities in response to the climate.

The approach can be utilised to estimate the effects of climate changes on the trees in a given stand. The requirements for the approach are in this case similar to those needed when approach is used to study the performance of tree and stand growth at geographically different locations. However, the treatment is simpler because one needs not to consider the genetic differences. In this case it is important to know how different processes can acclimate to environmental changes. The results of simulation for stands in South and North Finland suggest that small changes can be estimated quite readily even with the present approach. When the aspects such as variation in the annual cycle and summer droughts become important, they need to be considered in more detail. The method can be used to analyse how different structural adaptations, for example forking patterns, affect the performance of trees in very different conditions (see also Küppers 1989). In that manner, new information can be gained on the probable success of different genetic traits or different species in different conditions.

4.5 New important features of tree and stand growth suggested by the approach

The formulation of the model required construction of sub-models describing aspects that are poorly known. These aspects were studied through simulations. The sapwood turnover to heartwood, elongation growth and the forking patterns, nutrient uptake and retranslocation, the root competition, and the tree mortality had all a big effect on the simulation outcome when the parameter values of the sub-model describing these aspects were varied. Many of these aspects are such that their importance in the tree growth and stand development is not apparent. The used approach raises those as interesting hypotheses of factors affecting tree and stand growth.

An adequate description of growth and branching of shoots is an important factor determining the tree growth. Equations (19) and (20) in Chapter 2.2.4 demonstrate that the growth of foliage biomass implies an exponential demand for the mechanical and physiological support of shoots (also, e.g. Ford 1985). The exponent n that describes the dependency of shoot wood growth from foliage growth has a theoretical value of 3/2 for a single shoot in Equation 19. However, the value of n decreases when many daughter shoots grow from one mother shoot. The needle mass is distributed among many shoots and the average length of shoot per needle mass grows slower as would otherwise be the case. A minimum value is bigger than 1 since that value would give no length growth. The value of n has not much importance when the foliage mass per shoot is small since any exponent between 1 and 3/2 would produce almost the same outcome. However, as the amount of carbohydrates used for the growth of daughter shoots of a given mother shoot increases, the importance of this parameter becomes bigger. According to these considerations, very different allocation patterns could result between trees that have different branching design.

The branching pattern determines the extension growth of different parts of trees and the height growth, as well. It also determines the development of the light climate within the canopy and the relative position of the tree within the canopy. Also the extension growth relative to diameter growth has got a strong influence on the strength properties of wood (e.g. Ylinen 1952, Assman 1970, Morgan and Cannell 1988).

Kellomäki and Oker-Blom (1983) estimated that at high latitudes the within-crown shading of trees can be much more important than the between-tree shading. This should be considered when the costs and benefits of different branching patterns are studied. Küppers (1989) points out that it is not likely that the same pattern of growth can produce as good outcome from the cost-benefit point of view in all conditions. The branching pattern that was determined from young trees did not function so well in the simulations, as the trees became older. The allocation of carbon between stem and branches fluctuated and a very high proportion of carbohydrates was allocated to branches. There seems to be plasticity in the branching pattern of trees depending on the stage of the development of the stand (Ford 1985). The simulation results suggest that such plasticity is an important factor in stand growth.

The identification of differences in the branching pattern could be the easiest in conditions of very good growth. Then the differences in the biomasses would be the biggest between the branching patterns, both in absolute and relative terms. However, measurements only in these conditions could give biased results, since the plastic response to changing environment seems to be an important factor, especially as the trees age. The fact that there are obvious cost differences in shoot growth and obvious benefit differences because of between shoot shading can facilitate analyses of optimal branching patterns. These analyses could be used to aid for example tree breeding programmes.

Factors that affected heartwood formation had a large effect on the outcome of the simulation, as also demonstrated by Mäkelä (1988). Factors affecting crown dynamics had a big effect on the simulation results because heartwood formation depended on the crown dynamics. The effect was clear on the growth of foliage but rather small on woody growth. Changing the factors that affected the pruning limit of the model "crown" affected the timing and the level of needle mass culmination. On the other hand, changing the heartwood formation parameter of a branch affected mainly the needle mass of the later phases of stand development. In both cases the parameters had remarkably little effect on the wood formation. On the other hand, the model "branch" was sensitive to parameters that determined the self pruning of the trees and how the new needles at different heights reused the released transport structure [Chapter 2.2, Equation (25),].

Equation (18) in Chapter 2.2 shows that the changes in relative senescence rates directly affect the distribution of carbohydrates between the tree parts. The simulations demonstrate that small changes in the rate of heartwood formation change the allocation of carbohydrates between the parts of trees. When the foliage biomass is much affected, the changes in woody mass can be small. Those changes in the allocation pattern could explain why atmospheric pollution causes needle loss of conifers but does not reduce the stem wood growth as much (Nöjd 1990).

An adequate description of the "internal circulation of structure" seems to be important in determining the stand level growth of biomass compartments as well as the within tree distribution of foliage in the crown. I use the term "internal circulation of structure" to describe how the existing structure that the dying needles release is fulfilling the physiological and mechanical support requirements of the remaining and new needles (see also Figure 5). The use of the term is justified, since the process is analogous to the internal circulation of nutrient. No structure moves physically from one place to another in the process but the remaining needles start to use it similarly as the nutrients are used in the retranslocation process.

It is difficult to describe in exact terms the amount of existing transport capacity that comes to reuse from the dying needles at one height. To do this one would need to calculate the amount of sapwood that there is at different positions along the transport path before the growth begins. The transport path requirement for each height would then be the differences between the sapwood area that is required by the new total needle mass at each height and the existing sapwood area over the length of the transport path. This naturally requires a good description of the architecture of trees, i.e. the position of branches relative to other branches and stem. It is probable that the problems of sensitivity of the model to the reuse parameters stem partially from an inadequate description of the tree architecture.

Although there is empirical and experimental evidence for the existence of a relationship between heartwood formation and the death of whorls of branches (e.g. Kaipiainen and Hari 1985), more work is needed to study the generality of these observations and the mechanisms bringing them about. It seems strange that despite the big importance of these questions, little attention has been paid to them as reviewed by Saranpää (1990).

The presented role of existing structure on growth raises interesting aspects on the interpretation of trees as modular organisms. It has been argued that individual branches would be quite independent with respect to carbon (e.g. Sprugel et al. 1991). Plants can also be considered to consist of foliage and fine roots and associated infrastructure required for their functions as suggested by the concept of integrated physiological units (IPU, Caspar and Watson 1984). In such a case, the construction of the infrastructure at other parts of the plant needs to be considered as a necessary expenditure for each leaf element. In the presented approach, on the other hand, dying needles release transport structure that fulfills a big proportion of this structural requirement. Thus, a considerable amount of the photosynthetic products is liberated for other uses. So, in a way, the released transport structure is comparable to photosynthetic production that is transported by the tree to a particular location. Consequently a single shoot would not be independent even with respect of carbon, since the preexisting structure determines its growth potential to great deal.

The above considerations can have interesting consequences on the growth of trees in different light climates. In open grown trees the needlemass is growing or remain quite constant even in the lower branches. From this it follows that branches at different heights are utilising the transport structure released by the dying needles at that height. Naturally the shoots at the upper part of the tree have to use considerable amount of the carbon resources for the growth of stem, since there are hardly any senescing needles that release transport structure for reuse. The trees that are growing in closed canopies have continuously a big proportion of their crown in strong shade. In these parts the needle growth is considerable smaller than needle senescence. Therefore a big proportion of the transport capacity formely used by the foliage of the shaded crown is released for reuse by the upper crown. The needles growing there can thus use more of their resources for the shoot growth. So the "internal circulation of structure" between various needle generations could, at least partially, explain the height growth pattern of trees grown in different densities.

The root competition had a clear effect on the stand development. The simulated standing stock was 70% smaller when the "root extinction" coefficient was 0.0004 as compared to the stock obtained when using the value of 0.0002 for the coefficient. The effect on the needle mass was much more moderate. Competition between the roots seemed to decrease especially the value of peak needle mass at the canopy closure so that at the value of 0.0004 no clear peak was present. As Mäkelä (1990b) pointed out, the general trend in the growth of the different biomass compartments at stand level is a direct consequence of the diminishing returns of the growth of uptaking organs and the increasing cost of supporting organs according to the pipe model. By introducing the root competition, there is an independent decrease of uptake efficiencies of both nutrients and carbon per unit mass of uptaking organ. The distribution of growth results then so as to balance these changes. As can be seen from Figure 19 C the effect on allocation can be considerable.

The system started to oscillate before a stable development was found. This could indicate that the assumption of constant nutrient concentration in tissues does not allow a flexible enough response to strong changes. On the other hand it could be a question of inadequate time dynamics in the model. For the sake of simplicity, the level of root competition in the model depended on the fine root biomass of the previous year. This can generate unbalances in the system, specially during strong competition around the canopy closure.

Retranslocation of nutrients had a similar strong effect on the stand development as the "recycling" of the structure from senesced needles to the remaining and new ones. The effect was strongest on the fine root and stem masses whereas the foliage mass was less affected. Retranslocation especially affected the amount of carbon allocated to fine roots during the stable phase of the stand development. During that phase a considerable proportion of the nutrients for growth came from internal circulation in the simulations.

The simulations indicate that the internal circulation of nutrients is an important source of resources for long living plants (see also Nambiar 1985; Schulze and Chapin 1987; Helmisaari 1990). However, relatively little is known about the processes controlling the retranslocation of nutrients. The presented approach can facilitate the study of optimal needle senescence patterns from the new growth point of view. This may give some new insight on the role of internal nutrient cycling in the control of growth. Some experimental results suggest that unfavourable environmental conditions do not necessarily enhance the proportion of nutrients retranslocated from the senescing structures (Nambiar 1985, Schulze and Chapin 1987). However, the approach used in the present work could identify beneficial internal circulation patterns. These could then be used as a basis for experimental work to analyse, e.g., the success of certain individuals, provenances or species.

The importance of internal circulation of nutrients naturally emphasises the importance of leaching of nutrients from plants point of view. According to Chapin (1991) leaching can account for about 15% of the annual nitrogen and phosphorus returned from plants to soil. The simulation results suggest that it is an important factor determining plant growth.

An interesting result of the simulations was that the model was very sensitive to the parameter for nutrient uptake at the range of values that produced stand development comparable to the growth and yield tables. Especially at the lower range, a 40% increase in the parameter value (from 0.007 to 0.01) increased the allocation of carbohydrates to stem about two folds at the stable phase of stand growth. A change from 0.014 to 0.018 changed the allocation only by about 20%. This might reflect a high sensitivity of infertile stands to factors that further drop the availability of nutrients, such as forest fires and acid deposition.

Fertilisation experiments in Sweden have demonstrated that stand level fine root biomass is quite stable at very wide range of nutrient availabilities (Linder and Axelsson 1982). In simulations the fineroot biomass first increased as the nutrient availability was improved and then started to decrease again. At the range of values that corresponded to Calluna- to Myrtillus-type stands the actual fine root biomass was quite stable though, since the culmination of fineroot growth occurred at that range.

The modelling approach assumes a constant nutrient concentration in the tissue. As mentioned, the results by Tamm (1989) indicate that the concentration of nutrients in needles remains quite stable at different nutrient availabilities. However, as the nutrient availability increase, also the stable concentration increases. Considering the above in the model could decrease even further the changes in the stand level fine root biomass.

The mortality of trees is probably the process that is the most difficult to describe in adequate terms at the moment. Generally tree mortality has been attributed to a declining relationship between the need and availability of resources. The presented approach could work out if a stand was treated on an individual tree basis. The problems would be associated with the description of environment by trees and the genetic composition of the stand.

A model that uses tree size classes faces the problem that one should be able to describe population level phenomena within each size class. In the present model, this is done so that the proportion of trees dying in a given size class increases as the growth of needle mass falls beyond some threshold level. In qualitative terms the model functions satisfactorily even with the four size classes used in the model "crown". However, in this case it is extremely sensitive to the threshold level parameter. The sensitivity to the threshold level parameter decreases, though, as the number of size classes is increased. In any case improving the mortality component in the approach is very important.

4.6 Final remarks

The main aims of this work were to develop a theoretical framework for the growth of Scots pine and to test the applicability of the concept of balanced internal state, as described by the functional balance and the pipe model conditions, within this framework. These key assumptions were used to formulate a more general theoretical framework in the form of mathematical model. The general formulation of the growth processes as means of matching the tree structure with function was compatible with some of the other main theories in the field of physiologically based tree growth analyses. A simplistic approach was used in the mathematical formulation but also flexibility to more complicated formulations were identified.

The relationship between the transport structure and the foliage quantity was linear within a stand, but considerable between site variation was observed. The geographical variation suggested changes in the woody fine structure between sites. Also, the possible role of woody structure in the water balance of tree was identified. The analysis showed that a linear relationship does not describe exactly the relation between the growth of foliage and wood in all locations but the measurements between the change in the foliage mass and the tree ring area suggested that it could serve as an approximation of the relationship within the framework.

Testing of the approach showed that it can be applied to describe the stand dynamics within limited climatic conditions with only slight modifications. The application of the approach to a more general description of growth and yield of Scots pine in different climatic conditions requires additional work. Especially the role of acclimation and adaptation to environmental variations in the woody growth needs to be clarified more, as that has rather an important significance on the relationship between the growth of foliage, wood and fine roots.

The approach indicated that although the input/output reactions are important, also the rather weakly understood processes bringing about internal circulation of nutrients, and internal circulation of structure have big importance in the growth outcome. Also the connection between foliage growth and extension growth of shoots affect overall growth and stand development. Presently many of these factors were included into the analysis in a rather simple form. Therefore not much can be said about how, e.g., environmental change will affect them. However, the analysis shows that if there are changes in these processes, strong changes can also be expected in growth. Furthermore, the reason for changes in the growth could be the changes in the above factors.

The main justification for this work was derived from the need to estimate growth of tree stands in present conditions where the traditional methods of modelling growth become less applicable. It can be appreciated from this work, that it is not the best tool to estimate short term growth for management purposes. The problems involved in the correct determination of parameter values alone introduce bigger error to the analysis than normally accepted in forest management planning. However, as the planning period increases in length, the applicability of the approach improves since the accumulation of error is considerably less than in the traditional method. Similarly, when it is foreseeable that the conditions of the past and the future are not the same the traditional method looses its ground. Although nobody can predict the future, splitting the growth into its components facilitate intelligent guesses.

The main value of this type of work is that it can help us to understand complex forest ecosystems and the role of growth in them. As such it can help even the management level planning. It is possible, e.g., to identify which dimensions of tree to measure for an efficient estimation of growth. As mentioned, the parameter estimation of a model based on physiological processes is difficult. However, by linking the different factors together, it is possible to connect the growth process of tree to some readily measurable dimension (e.g. Sievänen 1992). Then it is a question of quantifying this relationship with simple regression techniques. In optimum case also the range of applicability of such relationship could be examined with the more theoretical model. Also this type of approach offers a tool to evaluate the outcome of different kind of thinning regimes. Even if the simulation results could not yet be used as direct quantitative estimations, they can point out hypothesis which could be tested with relatively short time experiments.

The rather aggregated method to study processes bringing about growth presented in this work offers means to study the dynamics of stand growth caused mainly by the stand development itself, i.e. the change in the size and number of individuals and the total biomass of different biomass compartments at stand level. As such it offers a tool for improving our understanding on the relative importance of processes bringing about stand development. A generalisation of this kind of model requires either determination of parameter values for different locations or more detailed analyses of the mechanisms bringing about the growth guiding principles. It is necessary that the changes in the principles can be derived as a function of both environmental and internal factors. The value of this approach is that it offers relatively a simple framework which can be readily adapted and extended to be used for making stand growth models for different purposes as contrast to the more flexible but simultaneously more complex mechanistically based models. At minimum, it offers a tool to analyse the importance of various factors in the growth phenomena.

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Seloste

Analyysi männyn kasvusta: rakenteen sopeutumista aineenvaihduntaan

Tässä työssä analysoidaan männyn kasvua osana puun elintoimintoja. Muuttuva ympäristö muuttaa puiden toimintoja. Toisaalta metsätaloutta harrastetaan alueilla, joiden metsien kehityksen luontaista dynamiikkaa ei tunneta. Edellä mainituista seikoista johtuen menneen puuston kehitykseen perustuvat kasvun ennustamismenetelmät menettävät käyttökelpoisuuttaan. Ainetaseisiin perustuvat kasvumallit tarjoavat vaihtoehdon. Niiden käyttöä rajoittaa eräiden perustavaa laatua olevien elintoimintojen huono tuntemus. Ongelma voidaan ratkaista olettamalla, että huonosti tunnettujen prosessien seurauksena syntyy havainnoilla tai esimerkiksi evoluutiokehityksellä perusteltavia säännönmukaisuuksia.

Esitetty lähestymistapa männiköiden kasvun mallittamiseen tarkastelee mäntymetsikköä ekosysteeminä. Ekosysteemikuvauksesta johdetaan yksinkertaistavien olettamusten avulla kasvun matemaattinen malli. Lähestymistapaa evaluoidaan kahdella tasolla. Erikseen tutkitaan yhden tärkeimmän yksinkertaistuksen pätevyyttä ja tämän jälkeen verrataan mallisimulaatioiden tuloksia havaittuihin metsiköiden kehityssarjoihin. Tämän lisäksi tarkastellaan mallin herkkyyttä eräiden, huonoimmin tunnettujen ilmiöiden suhteen. Lopuksi tarkastellaan lähestymistavan käyttökelpoisuutta kasvun analyysissä.

Metsäekosysteemi kuvataan hierarkisena kokonaisuutena (kuva 1). Puiden elintoiminnot jaetaan aineen vaihtamiseen kasvin ja ympäristön välillä ja kasvin sisäisiin reaktioihin. Jälkimmäisiin lasketaan aineiden kuljetus, niiden muuntaminen erilaisiksi kemiallisiksi yhdisteiksi ja niiden kulutus kasvuun. Elintoiminnot muodostavat hierarkisen systeemin, jossa kasvin sisäinen tila ja rakenne vaikuttavat hetkittäisiin vaihtoreaktioihin yhdessä hetkellisen lähiympäristön kanssa. Toisaalta sisäinen tila muuttuu hitaasti vaihtoreaktioiden tuloksena ja rakenne kasvaa asteittain muuttuvan sisäisen tilan perusteella. Edellä mainittujen reaktioiden vasteet systeemissä tapahtuviin virtauksiin määräytyvät geneettisen säädön tuloksena.

Teoreettisen viitekehyksen pohjalta laadittiin matemaattinen malli, jonka avulla lähestymistapaa arvioitiin. Kirjallisuustarkastelu osoitti, että sisäiset reaktiot ovat huonosti tunnettuja. Ongelma ratkaistiin olettamalla, että kasvin säätää toimintaansa niin, että sen sisäinen tila pysyy jatkuvasti tasapainossa. Tasapainoinen sisäinen tila kuvattiin puun ositteittain vakioisina ravinnepitoisuuksina. Toisaalta rakenteen ja puun sisäisten kuljetusprosessien oletettiin olevan tasapainoisia, kun neulasten ja vettä johtavan puuaineen poikkileikkausalan välillä vallitsi lineaarinen riippuvuus. Vaihtoreaktioiden nopeudet voitiin olettaa riippuvan pelkästään ulkopuolisista olosuhteista vakion sisäisen tilan olettamuksesta johtuen. Varjostuksen vaikutus fotosynteesiin ja juuristotihyeden vaikutus ravinteiden ottoon kuvasivat metsikkötason vuorovaikutukset.

Yhteisistä peruslähtökohdista laadittiin kaksi mallia. Niin sanotussa ”Crown” mallissa oletettiin kasvun määräytyvän puun keskimääräisten dimensioiden pohjalta. Sen sijaan mallissa ”Branch” puun kasvu muotoutuu yksittäisten versojen kasvun summana. Kuitenkin oletettiin, että latvustasolla saavutetaan optimaalinen versojakauma hiilen käytön suhteen. Molempien mallien yhteiset perusyhtälöt on esitetty yhtälöissä (1)–(18) ja (25)–(32). Näiden lisäksi liitteet 1 ja 2 esittävät pelkästään jommassa kummassa mallissa esiintyvät yhtälöt. Liitteissä 3 ja 4 on esittetty mallien yksinkertaistettu rakenne ja eri yhtälöiden väliset yhteydet. Lisäksi niissä on esitetty kummankin mallin vaatimat simulointien lähtötiedot. Lopuksi liitteesä 5 on esitetty mallien parametriluettelo ja mallisimuloinneissa käytetyt parametriarvot ja ne lähteet, joista arvot on saatu.

Lähestymistapaa testattiin kahdella eri tavalla. Toisaalta arvioitiin neulasmassan ja puuaineen poikkileikkauspinta-alan välisen lineaarisen riippuvuuden yleisyyttä ja toisaalta verrattiin simuloimalla saatuja tuloksia havaintoihin metsiköiden eri osien ja dimensioiden kehittymisestä. Lineaarinen riippuvuus näytti kuvaavan neulasten ja puuaineen välistä suhdetta samoissa ilmasto-olosuhteissa silloin, kun puuaineen poikkileikkauspinta-ala mitattiin fysiologisesti vastaavalta korkeudelta eri puissa. Havaittiin myös, että kyseisen riippuvuuden hajonta oli vähäisempää, kun mittaukset tehtiin maksimaalisen neulasmassan ajankohtana. Mittauksissa saatiin myös neulasmassan muutoksen ja puuaineen poikkileikkauspinta-alan muutoksen välille lineaarinen riippuvuus. Tämä tulos perustui tosin vain yhden eteläsuomalaisen ja yhden etelävenäläisen puun mittauksiin. Esitettyjen tulosten kuitenkin tulkittiin tukevan käytettyä yksinkertaistavaa hypoteesiä.

Erilaisissa ilmasto-olosuhteissa tehdyt mittaukset antoivat hyvin erilaisen kulmakertoimen sekä neulasmassan ja oksan poikkileikkauspinta-alan että latvuksen oksien poikkileikkauspinta-alojen summan ja latvuksen alarajan poikkileikkauspinta-alan väliselle riippuvuudelle. Tuloksen arveltiin ilmentävän eroja puuaineen hienorakenteessa, mutta myös pohdittiin mahdollisuutta, että puuaineen ja neulasten määrän suhteella olisi tärkeä rooli puiden vesitaloudessa. Tehtyjen mallien yleisempi käyttö erilaisissa olosuhteissa vaatineekin tarkempaa selvitystä puuaineen hienorakenteen ja sen toiminnan välisestä suhteesta Myös sopeutumisen ja mukautumisen merkitys puuaineen muodostumisessa identifioitiin tutkimuksen painopistealueeksi, jos halutaan ennustaa puiden kasvua erilaisissa ilmasto-olosuhteissa.

Simulointitulokset vastasivat Etelä-Suomen metsiköiden kasvun kehityssarjoja sillä parametrikombinaatiolla, joka oli laadittu vastaamaan mahdollisimman hyvin Pohjois-Hämeen olosuhteita. Toisaalta Lapin ja Etelä-Suomen metsien kasvuerot seurasivat kun aineenvaihto parametrit kerrottiin keskimääräisellä Pohjois-Suomen ja Etelä-Suomen kasvukausien pituuden välisellä suhteella sekä puuaineen ja neulasmassan väliselle suhteelle käytettiin paikallisesti mitattuja arvoja. Vastaava yritys Etelä-Venäjän metsiin ei antanut yhtä hyviä tuloksia. Kuitenkin havaittujen ja simuloitujen runkotilavuuden kehityssarjojen erot olivat pieniä verrattuna siihen, että neulasmassa/puuaine-suhteita ei muutettu vastaamaan Etelä-Venäjän olosuhteita. Mallia voidaan hyödyntää eri olosuhteisiin, jos parametrien arvojen muutokset tunnetaan. Mallin yleisempi sovellutus eri olosuhteisiin vaatii kuitenkin parempaa tietämystä mukautumisen ja sopeutumisen välisistä rooleista.

Simulointitulokset osoittivat mielenkiintoisia piirteitä metsikön kasvuun vaikuttavista seikoista. Tulosten valossa näyttää selvältä, että metsikön kehityksen kuluessa hiilihydraattien jakautuminen puun eri osien välillä muuttuu voimakkaasti. Tulokset viittaavat myös siihen, että ravinteiden sisäisellä kierrolla ja tavalla, millä usean sukupolven neulaset hyödyntävät saman puuaineen vedenkuljetuskapasiteetin, on ratkaiseva merkitys metsikön kehityksen kannalta. Myös versojen pituuskasvu- ja haaroittumistavalla oli selvä vaikutus metsikön kehitykseen. Tulosten valossa näyttäisi siltä, että niillä tekijöillä, jotka vaikuttavat ainetta vaihtavien kasvin osien toimintaan tai kuolleisuuteen olisi voimakas vaikutus varsinkin rungon kasvuun. Toisaalta ne seikat, jotka aiheuttavat sydänpuun muodostusta, haijastuvat lähinnä ainetta vaihtavien osien kasvuun. Tämä tulos saattaisi liittyä myös havaintoihin puiden harsuuntumisesta.

Käytetyn lähestymistavan arvo on ennenkaikkea siinä, että se voi parantaa meidän ymmärrystä niistä metsikön kehityksen aikaansaamista muutoksista, joilla on selvä vaikutus kasvuun. Sitä voi myös käyttää pienellä vaivalla muodostettaessa hypoteesejä kasvuun vaikuttavien tekijöiden merkityksestä metsikön kehityksen kannalta. Tämän tyyppiset mallit voisivat olla myös apuvälineinä, kun halutaan laatia parempia regressio-malleja nykyisten puiden dimensioiden ja niiden kasvun välille. Toisaalta lähestymistapa tarjoaa paremmin perusteltavissa olevan lähtökohdan pitkän ajan kasvun ennustamiseksi muuttuvissa ympäristöolosuhteissa.

Appendix 1. The equations of the model "Crown" not presented in text

Needle area density in the crown:

$$\chi(z) = \phi^* \left(\frac{z - h_{cb}}{h_t - h_{cb}} \right)^p \left(\frac{h_t - z}{h_t - h_{cb}} \right)^q C \qquad \text{(Al)}$$

where ϕ^*, (m^2/kg) is the average specific leaf area , h_t the height of the tree and h_{cb} the height of the pruning limit. p and q are parameters defining the shape of the crown and C (kg/m) is a scaling factor.

Average height of the stem weighed by the needle mass distribution:

$$h_{med} = \frac{\int_{h_{cb}}^{h_t} \chi_n(z) z \, dz}{W_n} \qquad \text{(A2)}$$

where $\chi_n(z)$, kg, is the needlemass at height z and W_n is the needlemass of the tree.

Height growth:

It was assumed that the height growth of a tree depended linearly on the diameter growth when trees were growing in open conditions without light competition (Ek 1971). The increasing stand density was assumed to increase this ratio (eg. Kellomäki and Kanninen 1980). Thus:

$$\Delta h = \Delta d_s (\beta_{hd} + DI) \qquad \text{(A3)}$$

where Δd_s is the diameter growth, β_{hd} is the ratio between the diameter at breast height and the height of open grown trees and DI is the density index.

Diameter growth:

Diameter growth is derived from the foliage growth and senescence considering that a part of the senescing foliage does not liberate transport structure to reuse (see equations (12)–(14) in the text). Thus:

$$\Delta d_s = \left(\frac{\sqrt{\left(4\left(G_n - R_f\right)\varepsilon_{st} + \pi d_s(k)^2\right)}}{\pi} \right) - d_s(k) \qquad \text{(A4)}$$

where G_n is the needle growth, R_f is the fraction of needle senescence that releases transport structure to reuse by the new needles (see equation (A12)), ε_{st} is the parameter relating needlemass with sapwood area and $d_s(k)$ is the initial diameter of the period.

Density index:

The amount of increase of the diameter height ratio depended on the steepness of the light gradient between the center of the upper third of the crown and that of the lower third. Thus:

$$DI = \beta_l \left(e^{-kY_n(uq)} - e^{-kY_n(lq)} \right) / \left(h_t - h_{cb} \right) \qquad (5)$$

where $\beta_{1,}$, (m), is the light gradient steepness factor, Y_n(uq) is the stand needle biomass above the center of upper third of the crown and Y_n(lq) is the stand needle biomass above the center of lower third of the crown of the representative tree of the size class and k, (1/kg), is the light extiction coefficient written in biomass basis.

Branch length growth:

The growth of the average length of branches was calculated in a similar fashion as the stem with the exception that density did not affect the relationship. However, since the average length of branch was used, also the effect of dying of the lower branches had to be considered. Thus:

$$\Delta l_b = \Delta d_b \beta_{ld} + (1 - k_{lr}) l_b \qquad \text{(A6)}$$

where Δl_b is the average length growth of branches, Δd_b is the average diameter growth of branches, β_{ld} the length diameter ratio of branches and K_{lr} is the reduction in the average length of branch due to self-pruning of tree.

Branch diameter growth:

The branch diameter growth was calculated from the branchmass growth assuming a constant form factor and known number of branches. Thus:

$$\Delta d_b = \left(\frac{\sqrt{\left(G_b + W_b\right)} - \sqrt{W_b}}{\sqrt{\left(4\pi ff \gamma_b l_b n_b\right)}} \right) \qquad \text{(A7)}$$

where G_b and W_b are the growth of and the initial amount of the branch mass in the tree, respectively, γ_b is the density of branch wood (kg/m^3), ff is the form factor of branches and n_b is the number of branches per crown of tree.

Correction of average length of a branch due to senescence:

It is assumed that the crown consists of conical upper part and cylindrical lower part. The branch length is

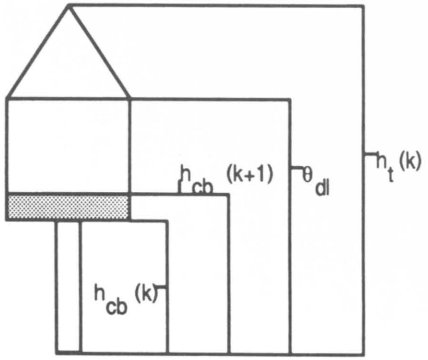

Figure A1. A schematic presentation of the dimension of the crown. The width of the crown is proportional to the length of the branches. $h_t(k)$ is the height of the tree, dl is the lower limit of the crown portion where branch length increase as a function of height and $h_{cb}(k)$ and $h_{cb}(k+1)$ are the pruning limits at two consequtive periods.

assumed to change linearly in the upper portions of the crown with the distance from the top but remain constant in the lower part. Self-pruning decreases the number of branches that have attained more or less a constant length (see Figure A1). Thus:

$$K_{lr} = \frac{h_t(k)/2 - h_{cb}(k+1) + \theta_{dl}/2}{h_t(k)/2 - h_{cb}(k) + \theta_{dl}/2} \qquad \text{(A8)}$$

where h_t is the height of the tree and h_{cb} is the height of the crown base, k refers to the initial conditions of the period and k+1 to the condition after growth, and dl is the lower limit of the crown where branch length growth takes place (see Figure A1).

Number of branches:

A constant number of branches was assumed to be formed each year. The number of dying branches was assumed linearly proportional to the pruning limit height change (see Figure A1). Thus:

$$n_b(k+1) = \left(\frac{h_t(k) - h_{cb}(k+1)}{h_t(k) - h_{cb}(k)}\right) n_b(k) + \beta_{pw} \qquad \text{(A9)}$$

where β_{pw} is the parameter giving the average number of branches per whorl and h and l are the height of the tree and the height of the pruning limit, respectively .

Root length growth:

Length growth of the transport roots was calculated from the fine root density of the stand. It was assumed that the fine roots of the same tree always fill new soil volume with the same density. It was also assumed that 50 % of the new fine roots are growing in the space already occupied by the transport roots and 50 % grow into new soil volume outside the circle occupied by the transport roots. Thus:

$$\Delta l_t = l_t + \left(\sqrt{\left((6.28lt)^2 + 6.28G_f / D_r\right)}\right) \Big/ 6.28 \qquad \text{(A10)}$$

where G_f is the fineroot biomass growth, D_r, (kg/ha), is a parameter describing the density by which the fine roots fill new soil volume. It is also the threshold density for the root competition (see equation 6).

Change of pruning limit:

It was assumed based on the optimality considerations presented in chapter 2.2.4 that the annual photosynthetic production of the needles at the pruning limit should be at least a certain proportion of the average annual photosynthetic production of the needles of the crown.The height of the pruning limit is thus determined based on the amount of light which has passed through the upper portions of the canopy and the position of the tree in the canopy. The photosynthetic production at pruning limit is a negative exponential function of the above needlemass at stand level. This yields the following equation:

$$\Delta h_{cb} = h_{\max} + \ln\left[\frac{P}{(P_0 \delta W_n)}\right] \cdot \left[\frac{(h_{\max} - h_{\min})}{\chi_{dr} \cdot (-k) Y_n}\right] - h_{cb} \qquad \text{(A11)}$$

where the logarithm term describes the required photosynthetic production and the term in brackets describes the light climate at the lower canopy. In the equation, h_{cb} is the height of the pruning limit and Δh_{cb} is the change in it. h_{max} is the maximum height of the stand and h_{min} the lowest present pruning limit of the stand, P is the annual photosynthetic production by the tree in question and P_o is the annual photosynthetic production of unit mass of needles in nonshaded conditions, W_n is the needle biomass of the tree and δ is a parameter giving the proportion of how much more needles can be grown per gram of assimilates at crown base than on average in the crown, χ_{dr} describes the ratio between the needle mass per unit height in the lower proportion of the canopy and that of the whole canopy. k , (1/kg) is the light extinction coefficient expressed at biomass bases and Y_n is the foliage mass of the stand.

Proportion of needle senescence that release transport structure for reuse:

The proportion of needles releasing transport structure in stem is assumed to depend on the crown dynamics (see eg.Hari et al., 1985; Kaipiainen and Hari, 1985). The needle biomass which died below the new pruning limit, (l(k+1)), is assumed not to release transport structure to reuse. In older trees heartwood is also formed on the branches which is assumed with a constant proportion of dying needles not releasing transport structure. Thus:

$$R_f = (1 - \sigma_b)\left(S_n - \int_{h_{cb}(k)}^{h_{cb}(k+1)} C y^p (1-y)^q \, dz\right) \qquad \text{(A12)}$$

where σ_b is the proportion of heartwood formation associated with the foliage senescence within a living crown and the second term in parentheses describes heartwood formation in stem due to self-pruning of trees. $h_{cb}(k)$ and $h_{cb}(k+1)$ are the pruning limit height at age k and k+1 and y is the relative height in the crown (see equation A1)

Nutrient uptake efficiency per unit amount of fine roots per year:

$$e_f = \begin{cases} e_f^* & \text{if} \quad Y_f \le D_r \\ e_f^* e^{-k_f(Y_f - D_r)} & \text{if} \quad Y_f \le D_r \end{cases} \qquad \text{(A13)}$$

where e_f^* is the nutrient uptake efficiency without competition effect, Y_f is the fineroot density of the stand and D_r is the threshold parameter indicating the initialization of competition (>0) and k_f , is the steepness of the slope describing the decrease in the nutrient uptake efficiency as a function of total fine root biomass of the stand.

Transport root senescence:

$$\sigma_{tr} W_{tr} = s_n \varepsilon_{tr} \gamma_{tr} l_{tr} \left(1 - \frac{(A_{tr}^{\max} - A_{tr})}{\varphi_{tr} + (A_{tr}^{\max} - A_{tr})}\right) \qquad \text{(A14)}$$

where A_{tr} is the average age of the transport roots, A_{tr}^{max} is the maximal age of transport roots and $_{tr}$ is a parameter that gives the age when 50% of the needle mortality causes proportional transport root senescence.

Appendix 2. The equations of the model “branch” not presented in the text

Specific Needle Area (Hari et al. 1982):

$$\phi(z) = c_1(c_2 - c_3 I(z)) \qquad \text{(B1)}$$

where (z) is the degree of interaction at height z (see equation (4) in the text) and c_1, c_2 and c_3 are parameters.

Height Growth (Hari et al. 1982):

$$\Delta h = f_1(P/P_0^*) f_2(\Delta\, d_{st}) f_3(A) \qquad \text{(B2)}$$

where

$$f_1(P/P_0^*) = 1 - \beta_{hg1} \frac{P}{P_0^*} \qquad \text{(B3)}$$

$$f_2(\Delta\, d_{st}) = \frac{\Delta\, d_{st}}{\beta_{hg2} + \Delta\, d_{st}} \qquad \text{(B4)}$$

and

$$f_3(A) = dh^* - dh_0(A) \qquad \text{(B5)}$$

where P is the photosynthetic production of a tree per unit needlemass and P_0^* is the same in unshaded conditions, Δd_{st} is the diameter growth and A is the age of the tree. β_{hg1} , β_{hg2} , dh^* and dh_0 are parameters.

Branch length growth (Nikinmaa and Hari 1990):

The length growth of shoots was treated slightly differently from the equation (20) and (21) of the text. The branching was treated as a stationary process which depended on the age and the branch length so that the exponent n of the shoot growth was 3/2 but that the value of the parameter, v, varied depending on the branch age and length. This yielded for the branch q:

$$\Delta l_{bq} = \begin{cases} \dfrac{b_1 G_{nq} + b_2}{(6!/(6 - A_b!)b_3 l_{bq}} & \text{if} \quad A_b < 6 \\ \dfrac{b_1 G_{nq} + b_2}{(6!)b_3 l_{bq}} & \text{if} \quad A_b \ge 6 \end{cases} \qquad \text{(B6)}$$

where A_b is the age of the branch, l_{bq} is the length of the branch and b_1, b_2 and b_3 are parameters.

Nutrient uptake efficiency per unit amount of fine roots per year:

$$e_f = \begin{cases} e^*_f & \text{if} \quad Y_f \le D_r \\ e^*_f \dfrac{D_r}{Y_f} & \text{if} \quad Y_f > D_r \end{cases} \qquad \text{(B7)}$$

where e^*_f is the nutrient uptake efficiency without competition effect, Y_f is the fineroot density of the stand and D_r is the threshold parameter indicating the initialization of competition (>0)

Distribution of released transport structure for reuse for growing needles (Nikinmaa 1987):

The released transport structure in the branches was assumed to serve the needles of the specific branch equally. That of stem was assumed to serve the needles of the specific height and those of all the above heights. This is modelled by assuming that the new needles at each height above the height at which the senescence took place would get a constant proportion of the released capacity for their use. This is formulated as follows:

$$\rho(h)=\int_{h_{cb}}^{h_t}\frac{\left(h-\zeta\left(h-h_t\right)\right)/h_t}{\int_{h}^{htop}\left(z-\zeta\left(z-h_t\right)\right)/h_t\,dz}S_n(h)\,\varepsilon_{st}\,\gamma_{st}\,h\,dh \quad (B8)$$

where ρ (h) is the released transport structure for height h, h_t is the height of the tree, h_{cb} is the pruning limit and ζ is a parameter giving the weight of the different heights; if its value is one all the heights are equally weighted, if it is less than one, the bottom part of the crown is favoured and if above one the upper parts of the crown are favoured. In the branch model ρ (h) is substituted for $S_n \varepsilon_w \gamma_w l_s$ of the equation (33) in the text.

Appendix 3. Structure of the model "Crown"

Initial states

Stand level data:
- Number of size classes
- Number of trees per size class
- Stand level biomass of needles, branches, sapwood, total stem wood, transport roots and fine roots

Data by the representative trees of each size class:
- Biomasses of needles by age classes, branches, stem sapwood and total wood, transport roots and fine roots
- Height, Pruning limit, Average length of branches, Average length of transport roots, Number of branches

Photosynthetic production

Summing the canopy needlemass (area) height distribution (Needle area distribution of a tree with Equation (A1))

Calculation of photosynthetic production by the representative tree with Equations (4) and (5)

Maintenance respiration

Mass of the biomass compartment times the specific respiration rate (Equations (6) and (7))

Determination of the biomass specific annual nutrient uptake

Equations (8) and (A13)

Pruning limit change

Equation (A11)

Senescence and transport structure release

Equations (25)-(30), (A12)

Growth

Distribution of growth between the biomass compartments, Equations (3), (11)-(14) and (18)

Stem diameter growth, Equation (A4)

Branch diameter growth, Equations (A7)-(A9)

Height growth, Equations (A3) and (A5)

Branch length growth, Equations (A6) and (A8), (A9)

Transport root length growth (A10)

Mortality of trees

Equations (31),(32)

End state (new initial states for period k+1)

Equation (1)

Appendix 4. Structure of the model "Branch"

Initial states

Stand level data:
- Number of size classes
- Number of trees per size class
- Stand level biomass of needles, branches, sapwood, total stem wood, transport roots and fine roots
- Minimum and maximum heights of the canopy

Data by the representative trees of each size class:
- Height and the pruning limit height
- Needle biomass per age classes per canopy height unit
- Branch length per canopy height unit
- Biomasses of branches, stem (sapwood and total), transport roots and fine roots
- Average length of transport roots

Photosynthetic production

Summing the canopy needlearea height distribution from the treewise mass distribution and from the specific leaf area Equation (B1)

Calculation of photosynthetic production by representative tree with Equations (4) and (5)

Maintenance respiration

Mass of the biomass compartment times the specific respiration rate (Equations (6) and (7))

Determination of the biomass specific annual nutrient uptake

Equation (8) and (B7)

Height growth and the transport root length growth

Equations (B1)-(B5) and (A10)

Minimum and maximum height of the canopy

Technical changes

Canopy layer divided into n slices of equal thickness, update of the slice a) length and b) position

Update of the foliage mass in the new slice (considering the changes in the slice)

Update of the branch length in the new slice

Senescence

Equations (25)-(30)

Distribution of released transport structure for reuse at different heights

Equation (B8)

Iterative search for constant κ in the Equation (32)

Set value for κ, either initial value or that from the previous period

Calculate the height distribution of the new needle biomass (Equation (34), (B6) for the exact shoot growth)

Calculate the biomasses of associated structures with Equations (11), (15)- (17) and (B6) for the shoot length growth

Compare the growth with the difference between photosynthetic production and maintainance respiration

If difference is unaccebtable (normally > 1-5%) change the value of and repeat until satisfactory result obtained

First gradient method is used in iteration and if it does not converge, then it is changed to Fibonacci method

Mortality of trees

Equations (31)-(32)

End state (new initial states for period k+1)

Equation (1)

Appendix 5. The parameter lists of models "crown" and "branch" with an example of sets of values

The parameter			Model crown	Model branch	Source
Name	Notation	Unit	Value	Value	
Unshaded annual photoprod.	P^*_0	kgC/kgDm/a	2.72	2.72	Korpilahti (1988)
Growth respiration	r_g	kgC/kgC(str.)/a	0.25	0.2	Mohren(1987)/Hari et al. (1982)
Maintenance respiration, needle	r_{mn}	kgC/kgC(str.)/a	0.18	0.2	Mohren(1987)/Hari et al. (1982)
Maintenance respiration,branch	r_{mb}	kgC/kgC(str.)/a	0.02	0.02	Schäfer et al. (1990)/ Mohren (1987)
Maintenance respiration,stem	r_{ms}	kgC/kgC(str.)/a	0.02	0.02	Schäfer et al. (1990)/ Mohren (1987)
Maintenance respiration, transport roots	r_{mtr}	kgC/kgC(str.)/a	0.02	0.02	Schäfer et al. (1990)/ Mohren (1987)
Maintenance respiration, fine roots	r_{mf}	kgC/kgC(str.)/a	0.9	0.6	Schäfer et al. (1991)/ Mohren (1987)
Carbon content, dry matter		kgC/kgdm	0.5	0.5	Linder & Axelsson (1982)
Nitrogen content of needles	π_n	kgN/kgdm	0.011	-	Mälkönen (1974)
Nitrogen content of branches	π_b	kgN/kgdm	0.004	-	Mälkönen (1974)
Nitrogen content of stem	π_s	kgN/kgdm	0.0007	-	Mälkönen (1974)
Nitrogen content of trans. roots	π_{tr}	kgN/kgdm	0.0013	-	Mälkönen (1974)
Nitrogen content of fine roots	π_f	kgN/kgdm	0.004	-	Mälkönen (1974)
Nutrient uptake per finerootmass	e_f^*	kgN/kgdm	0.006-0.02	-	Mälkönen (1974)
Nitrogen retranslocation %	ξ / π_n		70	-	Helmisaari (1990)
Threshold fineroot density	D_r	kg/m^2	0.1	-	Estimated fromPersson (1980)
Nutrient uptake "extinction" coefficient	k_f	1/kg	0.	-	
Nutrient demand (photoprod. x av. nutr. cont.)/ uptake efficiency		$(P/W_n)\ \pi / e_f$	-	0.1-1.6	Nikinmaa and Hari (1990), estimated from Mälkönen (1974)
Branch mass/ unit length/ needlemass	$\varepsilon_b \gamma_b$	m^{-1}	0.89	0.89	Hari et al. (1985), Kärkkäinen(1985),
Stem mass/ unit length/ needlemass	$\varepsilon_s \gamma_s$	m^{-1}	0.78	0.78	Hari et al. (1985), Kärkkäinen(1985),
Transport root mass/ unit length/ needlemass	$\varepsilon_{tr} \gamma_{tr}$	m^{-1}	0.45	0.45	Hari et al. (1985), Ilvesniemi (pers. com.)
Diameter height ratio of open grown trees	β_{hd}	-	25	-	Sievänen (pers. com.)
Light gradient multiplier	β_l	-	250	-	Estimated from volume tables
Light extinction coefficient in biomass bases	k	1/kg	0.0002	-	Stenberg (pers.com.)
Diameter/length ratio, branches	β_{ld}	-	100	-	Own studies (limited sample)
Branches per whorl	β_{pw}	-	4	-	This study
Lower limit of conical part of crown	θ_{dl}	-	0.4	-	Own studies (limited sample)
Needle growth per gram of carbon at crown base/ on the average in the crown	δ	-	2	-	Estimated from model "branch"
Needle density on the average in the crown/ that at crown base	χ_{dr}		0.5	-	Estimated, Ilonen (1981)
Needlemass mortality proportion by age classes:					
1	σ_{n1}		0.05	0.-0.1	Estimated from field data
2	σ_{n2}		0.1	0.1-0.6	
3	σ_{n3}		0.4	0.2-0.9	
4	σ_{n4}		1.0	1.0	
Proportion of needle senescence associated with heartwood formation in branches	σ_b		0.1	0.1	Estimation
Senescence of transport roots	σ_{tr}		-	0.1	Estimation

Maximum age of transport roots	A_{tr} max		150	-	Estimation
Senescence param. of transport					

The parameter			Model crown	Model branch	Source
Name	Notation	Unit	value	value	
root senescence model	φ_{tr}		15	-	Estimation
Senescence of fine roots	σ_f		1.0*	0.9	*Model assumption, see text, estimation , Persson (1980)
Tree mortality threshold parameter	m_t		1.0	1.0	Estimation
Tree mortality rate parameter	m_r		1.0	1.0	Estimation
Needlearea distribution parameters	p,q		1.0	1.0	Hari et al. (1982)
Specific needle area parameters	c1	g/dm^2	-	2.9	Hari et al. (1982)
	c2		-	1.0	"
	c3		-	2.0	"
Height growth parameters	β_{hg1}		-	0.4	"
	β_{hg2}	g	-	200	"
	dh*	cm	-	50	"
	dh_0	cm/a	-	0.3	"
Branch length growth parameters	b_1	m/kg	-	51.21	Nikinmaa &Hari (1990)
	b_2	m	-	0.016	"
	b_3		-	2.00	Estimated from limited data
Transport structure release weight parameter	ζ			1.0	Estimation

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