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EFIMOD 2—a model of growth and cycling of elements in boreal forest ecosystems

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Abstract

The model EFIMOD 2 was developed for the description of tree (stand) growth and biological turnover of elements in boreal and temperate forest ecosystems. The model has the following features. (i) It is a spatially explicit stand-level simulator for Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. Karst) and Pendula birch (*Betula pendula* L.) on different forest soils growing under different climatic conditions in Europe; each stand consists of individual trees for which growth is modelled depending on the tree's position within the stand and local light, water and available nutrient conditions. (ii) The model has a tree-based submodel for total biomass distributed between several biomass compartments. (iii) The calculations include natural regeneration as well as ground vegetation dynamics. (iv) The soil submodel (ROMUL) is used to assess organic matter dynamics and nitrogen availability for tree growth as a function of soil temperature, soil moisture content and litter quality. (v) EFIMOD 2 calculates nitrogen cycling and accounts for atmospheric nitrogen deposition, nitrogen fixation and leaching, vegetation uptake, litter fall and nitrogen redistribution within and between trees and soil horizons. (vi) Monte–Carlo simulations are done to simulate the extent of naturally oscillating variability.

EFIMOD 2 allows for short-term and long-term simulations of natural and managed forest ecosystem dynamics over a wide range of forest sites, climatic conditions and silvicultural regimes. The model calculates dendrometric parameters for every tree, including undergrowth and seedlings, total growing stock, and pools of coarse woody debris and soil organic matter, with special reference to carbon and nitrogen dynamics. The model is effective for assessing wood productivity and evaluation of forest management regimes to meet criteria and indicators of Sustainable Forest Management. This includes a general evaluation of biodiversity and soil sustainability. The model system allows for the direct use of standard forest inventory data. Output variables include carbon and nitrogen pools in the stand and soil, CO_2 emissions, and tree (stand) growth and yield.

Keywords: Individual-based model; Forest and soil dynamics; Carbon and nitrogen balance; Element cycles

1. Introduction

Simulation modelling, as a tool for forest ecosystem analysis, stands between the complex reality of the simulated system and a lack of measured experimental data to evaluate the model parameters. We

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define a forest ecosystem as a system that consists of the tree layer, ground vegetation layer, cohorts of natural regeneration, and pools of organic matter and nitrogen in the soil. These compartments respond to the impacts of the hydrothermal conditions of the environment, including air, litter and soil temperature, soil moisture, precipitation, as well as the physical and chemical properties of the soil.

The complexity of the natural "forest–ground vegetation–soil–atmosphere–water" system has led to corresponding complexity and great variety of simulation models (see reviews by Ågren et al., 1991; Liu and Ashton, 1995; Tiktak and Van Grinsven, 1995; Ryan et al., 1996; Smith et al., 1997; Battaglia and Sands, 1998; Chertov et al., 1999a). Simultaneous consideration of the complex interactions between interception of radiation by the trees' canopy, CO_2 uptake, soil nutrition and water use leads to evident difficulties in developing a well-balanced detailed model that can describe the interrelations between forest growth, soil dynamics and water regime for different purposes. Hence, any new model either should describe a new combination of the leading factors and restrictions to be applied to the solution of a new problem or should develop a new approach that allows for the study of new kinds of system's dynamics observed in nature and not explained in the existing models.

The approach described here was undertaken to provide a new model to simulate the effects of the main factors that determine stand growth and the cycling of elements in the forest ecosystems that is designed to use existing standard forest and soil inventory data. We assume that soil dynamics is crucial to forest ecosystem function and sustainability. Vegetation and soil are linked through the turnover of elements in the vegetation–soil system, where vegetation has a productive role and soil serves not only a destructive role but acts as a system buffer. The goal of this study is to construct a model so that it is able to forecast the consequences of climatic and environmental changes, pollution impacts, and forest management practices while avoiding, if possible, the significant uncertainties of forest and soil inventory data.

A simulation model for the cycling of elements in forest ecosystems should be able to (a) test hypotheses about the main processes in the ecosystem's compartments by comparison with experimental data; (b) evaluate carbon and nitrogen dynamics in boreal forest ecosystems as a function of site and climatic conditions; (c) establish correlation and uncertainties between the flow of elements and different compartments of the ecosystem, for example, carbon and nitrogen contents in soil with net primary production of the vegetation; (d) estimate ecosystem variables that are infrequently measured (i.e. CO_2 emission, mineral nitrogen); (e) analyse the consequences of the different types of cuttings; (f) analyse the consequences of silvicultural operations (fertilisers, soil amendments, burning of cutting residuals, etc.), and (g) analyse response of carbon and nitrogen dynamics to fires and insect attacks.

One unique feature of the proposed model's structure is a consideration of the stand as a set of separate trees with spatially explicit positions within the stand. This approach assumes a significant role for local interactions of a tree with a set of neighbours and requires allocation rules for continuously distributed external factors, such as temperature, light, soil water and nutrients. We assume that the growth of an individual tree should be defined in the simplest way instead of a detailed description of their growth at a physiological level. Then, the population statistics of a set of simple stochastic constituents can be used to describe the dynamics of averages and distributions of stand's characteristics (Komarov, 1980).

A simple approach to the description of tree growth and tree–soil interactions was presented by Chertov (1983a,b, 1990) and later developed by Chertov et al. (1999a,b, 2001). The main assumptions for the description of the tree were made from an ecological point of view based on its ecological characteristics, or "silvics". Silvics describe the species-specific characteristics of tree growth, development and response to environmental factors and resources. Information and data for biological productivity and eco-physiology were synthesised in order to quantify the tree ecological parameters. These parameters are different from the silvics used in traditional gap models (Paal et al., 1989; Prentice and Helmisaari, 1991).

The most important ecological parameters for trees in the EFIMOD model include:

1. Biological productivity of leaves/needles; $\alpha_{\max}(T_{\text{air}})$ *grams of biological production (biomass increment) per gram of leaf/needle per year*, where

T_{air} is annual air temperature. This parameter reflects the maximum net photosynthesis for a given climate with no limitations due to crown shadowing, soil moisture and/or soil nutrients. This concept links the growth of single trees with the net primary productivity of the ecosystem that is allocated to individual trees through competition for light and nitrogen. On the other hand, maximum biological productivity may be linked with climate through temperature conditions with the help of a scaling procedure similar to those commonly used in many gap models (Chertov et al., 1999a,b, 2001).

2. Specific consumption of soil nutrients; n_p (*grams of nutrient required for a gram of tree production per year*) (Chertov, 1983b). This parameter is necessary to calculate tree increment and is dependent on the available soil nutrient pool (N_m) as N_m/n_p. The parameter is an expression of the authors' approach to the concept of the "nutrient and nitrogen productivity" developed by Vitousek (1982), Ågren (1983) and Ågren and Bosatta (1996).

The core of our model is restricted to a few factors, including climate, light conditions within the stand, and carbon and nitrogen turnover. We omit, in this version of the model, the detailed consideration of water regime and assume that the simulated stands exist in optimal conditions for humidity and soil moisture. We do not consider the effects of soil drought or a high water table. The response to changes in weather is simulated through the soil submodel where the total amount of soil available nitrogen depends on the current weather and the amount of available nitrogen feeds back to alter tree growth.

The EFIMOD 2 model of the "forest–soil" system is based on the following basic assumptions:

- It is an individual-based spatially explicit model. Trees are located within the simulated plot on a square grid with cells that are sufficiently small to contain more than one tree.
- Each tree consists of five compartments (stem, branches, leaves/needles, coarse roots and fine roots) and possesses its own area of nutrition that varies with time.
- Each tree competes with the nearest neighbour trees for intercepted radiation due to shadowing and competes for available nitrogen uptake from the soil. Tree growth depends on the most limiting resource (intercepted radiation or available nitrogen).
- A Monte–Carlo procedure is available to simulate the stochastic character of climatic and soil inputs, and determine the initial patterns of trees on the plot.
- ROMUL, a model of soil organic matter (SOM) dynamics, is a substantial part of the EFIMOD 2 system.
- SCLISS, a special soil climate generator with a monthly time step, was developed to support ROMUL by providing the necessary air and soil meteorological data for standard and Monte–Carlo runs.
- Submodels for ground vegetation, natural regeneration and the soil processes of leaching and biological nitrogen fixation are included into the system of models.
- The model describes carbon turnover in the ecosystem, including SOM dynamics.
- Nitrogen turnover is explicitly accounted for in the different compartments of the forest ecosystem within the plot.
- A simple model of tree growth is used that accepts standard forest inventory data as model input parameters and does not require special experimental data.
- This computer simulation model has a user-friendly interface and uses an object-oriented approach that easily allows for the addition of new processes and extending the model for a wide range of applications.

The main experimental bases for the model compilation were studies on the biological productivity of Norway spruce (*Picea abies* L. Karst), Scots pine (*Pinus sylvestris* L.) and Silver birch (*Betula pendula* L.) in Russian boreal forests (Kazimirov and Morozova, 1973; Kazimirov et al., 1977, 1978) augmented by research results from Finland (Mälkönen, 1974, 1977; Kubin, 1983).

Thus, EFIMOD 2 provides the possibility to assess the effects of elements' supply on pure and mixed stand growth and carbon and nitrogen turnover in a forest ecosystem depending on tree position in the stand, climate and soil. The spatial explicitness of trees' positions within the stand allows for easy and rapid simulation all conceivable kinds of cuttings and their ensuing consequences.

A previous version of the tree–soil system's model (EFIMOD) using the same submodel of tree growth was published earlier (Chertov et al., 1999b) and produced realistic results (Chertov et al., 1999c). Detailed descriptions and testing of ROMUL (model of SOM dynamics) and SCLISS (soil climate generator) can be found in earlier publications (Chertov and Komarov, 1997; Chertov et al., 2001; Bykhovets and Komarov, 2002) and are not considered here.

2. Compilation of the system of models

2.1. Tree submodel

2.1.1. Model description

In the majority of gap and eco-physiological tree models actual growth of tree biomass usually is determined as potential growth that is subsequently modified by proportional growth multipliers where the magnitude of the multiplier depends on external conditions (i.e. Botkin et al., 1972; Kellomäki et al., 1992, 1993). We chose the growth multiplier according to Liebig's law of the minimum (Liebig, 1843), which states that the factor/resource that is in the shortest supply determines the system's production rate. It is assumed in this case that changes to other factors do not influence the growth rate. A flow chart of the model is shown in Fig. 1. Tree biomass increment is dependent on available Photosynthetic Active Radiation (PAR) after shadowing and the portion of soil nitrogen available for tree growth. Thus, two possible types of tree increment can be calculated; that due to light or that due to soil nitrogen. These values of tree increment reflect the influences of climatic and soil conditions. Their calculation requires species-specific estimates of leaf/needle and fine root biomass, maximal biological productivity of leaves/needles and the specific consumption rate of nitrogen. The minimum value of the two increments is selected following the Liebig's principle.

The total tree increment is allocated to different tree compartments using species-specific proportions that are different for each of three tree age classes (young, mean-aged and old). The total mass and nitrogen content of litter cohorts (leaf, root and branch) are calculated for every tree. Litter cohorts enter the soil as above- and below-ground cohorts that decompose as a function of climatic conditions and litter quality (nitrogen and ash content). The products of their decomposition form a pool of total SOM and its nitrogen content and a pool of available soil nitrogen that is used for plant growth. When a tree dies its dead wood and coarse roots are added as additional litter cohorts.

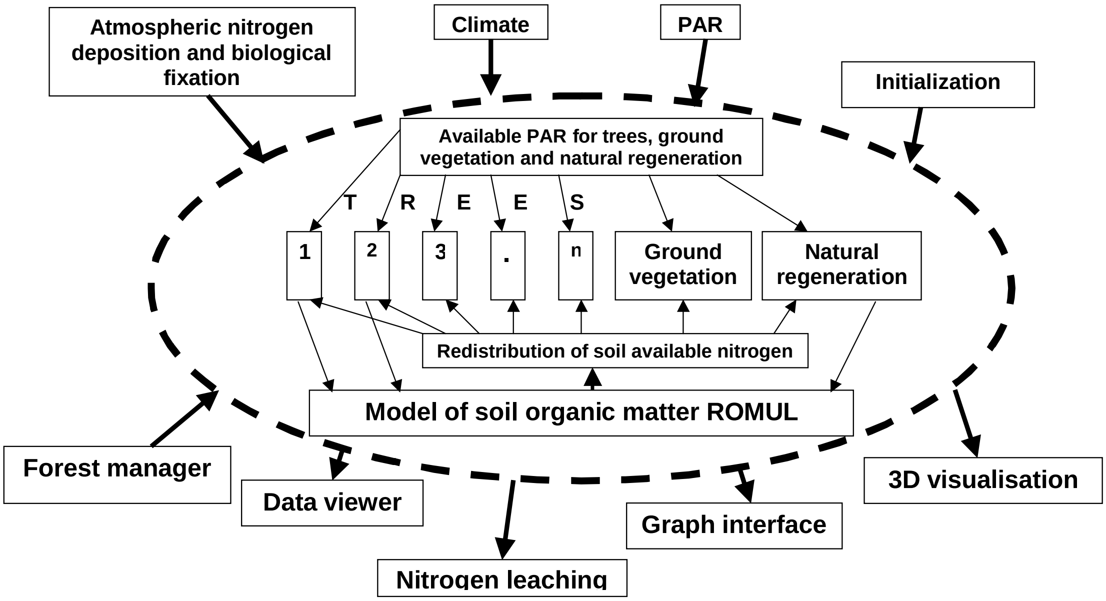

Fig. 1. Flow chart of individual-based spatially explicit combined model of tree–soil system EFIMOD 2.

The forest ground vegetation and cohorts of natural regeneration for each tree species receive their portion of available soil nitrogen and grow as a function of light conditions and nitrogen supply also using Liebig's principle. Their litter participates in the turnover of elements in the forest–soil system.

2.1.2. Basic equations

The single tree growth model is a simulator with the following five biomass compartments ($\mathrm{kg}_{\mathrm{dry\,mass}}$); leaves/needles B_l, branches B_br, stem B_st, coarse roots B_cr and fine roots B_rf. Total dry biomass for each tree B_T is calculated by summing all the compartments. I_p is the total tree increment ($\mathrm{kg}_{\mathrm{dry\,mass}}$ per year) and L_p is the total tree litter ($\mathrm{kg}_{\mathrm{dry\,mass}}$ per year). The main balance equation with time step $\Delta t = 1$ year is

$$\frac{\Delta B_\mathrm{T}}{\Delta t} = I_\mathrm{p} - L_\mathrm{p}. \tag{1}$$

Total tree increment I_p is calculated as

$$I_\mathrm{p} = \min\{I_\mathrm{pe}(\alpha_{\max}(T_\mathrm{air}), \mathrm{PAR}, B_\mathrm{l}); \\ I_\mathrm{pn}(N_\mathrm{T}, B_\mathrm{rf}, N_\mathrm{m}(T_\mathrm{soil}, W_\mathrm{soil}))\}; \tag{2}$$

where I_pe is the tree increment due to maximal biological productivity $\alpha_{\max}(T_\mathrm{air})$, light intensity (available PAR) and leaf biomass B_l. I_pn is the tree increment due to specific nitrogen consumption N_T, fine root biomass B_rf and available soil nitrogen $N_\mathrm{m}(T_\mathrm{soil}, W_\mathrm{soil})$ as a function of soil temperature and moisture. The expression under the minimum symbol is a formal expression of Liebig's law.

The increment due to light intensity I_pe is calculated as:

$$I_\mathrm{pe} = \alpha_{\max}(T_\mathrm{air}) B_\mathrm{l} K_\mathrm{SH}(\mathrm{PAR}), \tag{3}$$

where $\alpha_{\max}(T_\mathrm{air})$ is the maximal biological productivity of leaves/needles, B_l is leaf/needle biomass; $K_\mathrm{SH}(\mathrm{PAR})$ $(0 \le K_\mathrm{SH}(\mathrm{PAR}) \le 1)$ is the light response multiplier.

The increment due to available nitrogen I_pn is defined as:

$$I_\mathrm{pn}(N_\mathrm{T}, N_\mathrm{m}(B_\mathrm{rf}, T_\mathrm{soil}, W_\mathrm{soil})) \\ = \frac{(N_\mathrm{m}(B_\mathrm{rf}, T_\mathrm{soil}, W_\mathrm{soil}) + N_\mathrm{buffer})}{N_\mathrm{T}}, \tag{4}$$

where $N_\mathrm{m}(B_\mathrm{rf}, T_\mathrm{soil}, W_\mathrm{soil})$ is available nitrogen from the soil in the tree's area of nutrition (dependent on B_rf) at the current time step, N_buffer is nitrogen in the tree which may be reallocated and used for the growth of new plant tissues and N_T is the specific consumption of nitrogen (SCN) that is a species-specific constant. N_buffer is nitrogen that is withdrawn from senescing leaves and deposited in a tree (Vitousek, 1982; Aerts, 1996; Killingbeck, 1996). We assume that this buffer is used each year for growth.

2.1.3. The ecological parameters for each tree species

2.1.3.1. Maximal biological productivity of leaves/needles. As was mentioned before, $\alpha_{\max}(T_\mathrm{air})$ [$\mathrm{g}_{\mathrm{dry\,mass}}$ of biological production (biomass increment) per $\mathrm{g}_{\mathrm{dry\,mass}}$ of leaves/needles per year] reflects the maximum net primary production (NPP) of a tree. We postulate that $\alpha_{\max}(T_\mathrm{air})$ reflects maximal tree growth for all climatic conditions with no limitations due to crown shadowing, soil moisture and/or nutrients. The value of this variable is the ratio of biomass increment to leaf mass for the best site conditions. This implies expenditures of energy for photosynthesis, respiration, water and assimilates transport are integrated in the variable.

The relationship between $\alpha_{\max}(T_\mathrm{air})$ and growing degree-days (the sum of temperature on days with a mean daily value greater than 5 °C) for Scots pine, Norway spruce and Silver birch using data of Karpov (1969), Alexeev (1975), Chertov (1983b) and Kostin (1997) is shown in Fig. 2.

2.1.3.2. Specific consumption of nutrients. We defined the specific consumption of nutrient elements as the amount of element that is needed for the synthesis of one unit of tree biomass. The total SCN, N_T, is calculated as a weighted sum of the SCN (kg element per $\mathrm{kg}_{\mathrm{dry\,mass}}$ of increment) for the different tree compartments (i.e. n_s for stem, n_l for leaves/needles, n_b for branches, n_cr for coarse roots and n_fr for fine roots). If I_p is an increment of total tree biomass, then $I_\mathrm{s} = \alpha_\mathrm{s} I_\mathrm{p}$, $I_\mathrm{l} = \alpha_\mathrm{l} I_\mathrm{p}$, $I_\mathrm{b} = \alpha_\mathrm{b} I_\mathrm{p}$, $I_\mathrm{cr} = \alpha_\mathrm{cr} I_\mathrm{p}$ and $I_\mathrm{fr} = \alpha_\mathrm{fr} I_\mathrm{p}$ are increments of stem, needles/leaves, branches, coarse roots and fine roots, respectively, and α_s, α_l, α_b, α_cr, α_fr are the proportions of the total biomass

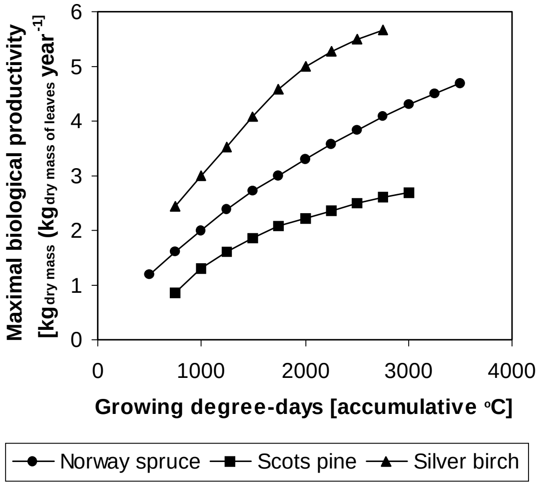

Fig. 2. Dependencies of $\alpha_{\max}$ on growing degree-days for different tree species. (▲) Silver birch, (●) Norway spruce, (■) Scots pine.

increment reallocated between compartments. Then,

$$N_{\mathrm{T}} = n_{\mathrm{s}} I_{\mathrm{s}} + n_{\mathrm{l}} I_{\mathrm{l}} + n_{\mathrm{b}} I_{\mathrm{b}} + n_{\mathrm{cr}} I_{\mathrm{cr}} + n_{\mathrm{fr}} I_{\mathrm{fr}} = (n_{\mathrm{s}} \alpha_s + n_{\mathrm{l}} \alpha_{\mathrm{l}} + n_{\mathrm{b}} \alpha_{\mathrm{b}} + n_{\mathrm{cr}} \alpha_{\mathrm{cr}} + n_{\mathrm{fr}} \alpha_{\mathrm{fr}}) I_{\mathrm{p}} \qquad (5)$$

The ranges of values of N_{T} (total nitrogen consumption) for boreal tree species were estimated from the experimental data of Kazimirov and Morozova (1973), Kazimirov et al. (1977, 1978) and Mälkönen (1974, 1977) and are shown in Table 1. The values of nitrogen consumption for different tree species' compartments are shown in Table 2. In this version of the model, we treat the values of n_i for different compartments as constant for the site and climatic conditions of European boreal forests.

2.1.3.3. Partitioning of biomass increment and tree age status. The rule's for redistribution of total biomass increment ΔB_{T} of a tree into increments for each tree's compartments is dependent on the tree's stage of development, i.e. young (pre-generative), mature (generative) and over-mature (post-generative). The proportion of the increment allocated to different compartments for different age classes (Table 3) were estimated from data published by Kazimirov and Morozova (1973), Kazimirov et al. (1977, 1978) and Ågren and Axelsson (1979).

2.1.3.4. Portions of litter in different compartments and corresponding nitrogen. Tree litter from different compartments for all species was estimated as a proportion of the compartment's total biomass (i.e. branches and coarse roots 0.0025 or fine roots 1.0). For leaves of deciduous species this proportion is equal to one. For coniferous trees the proportion of total needle biomass going to litter is the inverse of needle life-span that, in turn, depends on climatic conditions. In the central boreal zone, we estimated the value for annual needle fall for Scots pine at 0.25 and for Norway spruce at 0.15 (Kazimirov and Morozova, 1973; Kazimirov et al., 1977; Mälkönen, 1974, 1977). Using the experimental data just cited it is possible to discern the relationship between the proportion of needle litter fall, β, and climatic conditions. In general, as needle life-span decreases the proportion that goes to litter increases as the climate warms.

The nitrogen and ash contents of litter cohorts play significant roles in the soil submodel. The data necessary to run the model are species-specific parameters that, in most cases, can be found in the published literature.

Table 1
Specific consumption of soil nutrients N_{T} (kg elements per kg of tree increment) for different tree species and different elements in Finnish and Russian boreal forests (Kazimirov and Morozova, 1973; Kazimirov et al., 1977, 1978; Mälkönen, 1974, 1977)

Species	Range	N	P	K	Ca	Mg
Scots pine	Minimal	0.0035	0.0006	0.0017	0.0015	0.0006
	Maximal	0.0075	0.0032	0.0078	0.0109	0.0027
Norway spruce	Minimal	0.0040	0.0008	0.0027	0.0072	0.0007
	Maximal	0.0130	0.0045	0.0127	0.0540	0.0045
Silver birch	Minimal	0.0088	0.0008	0.0026	0.0049	0.0013
	Maximal	0.0262	0.0025	0.0074	0.0142	0.0040

Table 2
Specific consumption of soil nitrogen, n_i (kg nitrogen per kg of tree increment), for different tree species and different compartments (Kazimirov and Morozova, 1973; Kazimirov et al., 1977, 1978)

Tree species	Stem (n_s)	Leaves (needles) (n_l)	Branches (n_b)	Coarse roots (n_{sr})	Fine roots (n_{fr})
Scots pine	0.0014	0.0060	0.0040	0.0024	0.0047
Norway spruce	0.0022	0.0100	0.0050	0.0030	0.0055
Silver birch	0.0015	0.0200	0.0040	0.0045	0.0100

2.1.4. The calculation of available light and available nitrogen as a result of competition amongst the trees

Given the explicit spatial positions of trees within the stand, we have to define the rules for allocation of available resources between trees. We consider two kinds of competition for resources, first for light and second for available nitrogen.

The simulated sample plot is split into a grid of cells with size 0.5 m × 0.5 m. We assume that this size is sufficiently small to contain more than one tree. The use of grid cells allows the model to account for competition between neighbouring trees in discrete terms. The grid is used to calculate the cost of shadowing by a tree and to calculate a tree's zone of nutrition. The grid is a set of neighbouring cells that can vary with tree size.

In this version, the soil is assumed to be laterally homogeneous, i.e. all grid cells are described by the same soil variables. The available soil nitrogen is evenly distributed amongst all cells in the grid.

2.1.4.1. Growth reduction by light conditions. Light response multiplier, $K_{SH}(PAR)$, is a function of a shadowing coefficient K_E ($0 \leq K_E \leq 1$) and defines reduction of light intensity. The value of K_E is calculated for every tree in the simulated stand using a procedure that accounts for available light in each spatial cell as a shadow zone.

Competition for the light in EFIMOD 2 is modelled by a simple shadowing approach, which takes into account positions and sizes of neighbouring trees without calculation of direct light rays and absorption of radiation within the canopy. We use an integrative account of shadowing which allows us to mathematically describe competition for available light (keep in mind that the current increment of the tree is constructed using an integrated parameter as well).

Each tree creates a shadow zone S_i, which is a quadrate centred in the tree's cell x_i with quadrate size R_i. The tree x_i shadows the neighbouring tree x_j, if

1. the shadow zone S_i covers the tree's cell x_j, or
2. the ratio of the height H_i of tree x_i to the height H_j of a tree x_j is greater than a fixed value β, i.e. $H_i/H_i > \beta$.

Symmetric shadowing occurs when two trees shadow each other. The effect on a tree in the shadow formed by all trees shadowing the cell is assumed to be additive. Thus, for the shadow coefficient $0 \leq K_E \leq 1$ corresponding to the tree x_i,

$$K_E(x_i) = 1 - \sum \lambda_l k_l \qquad (6)$$

Table 3
Relative distribution of biomass increment by compartments in dependence on age status of a tree

	Age status (year)	Stem (α_1)	Leaves (needles) (α_2)	Branches (α_3)	Coarse roots (α_4)	Fine roots (α_5)
Scots pine	≤30	0.19	0.25	0.10	0.10	0.36
	31–130	0.37	0.20	0.11	0.12	0.20
	≥131	0.30	0.17	0.11	0.12	0.30
Norway spruce	≤30	0.20	0.30	0.10	0.10	0.30
	31–100	0.30	0.28	0.07	0.07	0.28
	≥101	0.26	0.33	0.04	0.04	0.33
Silver birch	≤20	0.40	0.30	0.09	0.06	0.15
	21–70	0.36	0.36	0.05	0.05	0.18
	≥71	0.24	0.44	0.04	0.06	0.22

where λ_l is a species-specific parameter describing the portion of PAR absorbed by the crown of the shadowing tree and k_l is the number of trees of certain species shadowing the tree x_i. Therefore, when one or more trees of the same or different species shade the same cell, then the total shadowing of the cell is the sum of their λ_l values. The values of λ_l were calculated using experimental data on the radiation absorbed under canopies of different tree species at maximal crown density (Tselniker, 1978).

The shadowing zone is assumed to increase in size as the height of the shadowing tree increases. It is important to realise that, strictly speaking, this definition of competition is not solely due to shadowing but is used as a way to describe the interaction of a tree with its nearest neighbouring tree that can be accounted for, in a generalised form, by relative illumination.

After the calculation of a spatial mosaic of shadowing (available light in every cell) the light response multiplier, K_{SH}, is calculated for every tree. The value of K_{SH}, as a function of shadowing, has a different shape for shade-tolerant and shade-intolerant species, i.e. K_{SH} is linearly dependent on K_E for Scots pine and Silver birch (shadow-intolerant trees):

$$K_{SH} = K_E;$$

and is non-linearly dependent for shadow-tolerant Norway spruce (Alexeev, 1975; Tselniker, 1978, p. 46):

$$K_{SH} = 1 + 0.44 \log K_E \tag{7}$$

Thus, the light response multiplier K_{SH} reflects the local stand density in relation to a set of neighbours for each tree in the form of overlapping zones of shadowing and species-specific response of trees to light.

2.1.4.2. Distribution of soil available nitrogen amongst trees in a stand.

The rules for distributing spatially continuous soil available nitrogen to trees reflect the sizes of the trees and their mutual arrangement within the stand. For each tree we define a zone of nutrition, which is the source from which a tree can draw upon for available soil nitrogen. Since the zones are allowed to overlap, rules had to be defined to redistribute available nitrogen from a grid unit if that unit belongs to more than one tree's zone of nutrition.

The zone of soil nutrition of an individual tree Z_i is modelled by a "pseudo-disc" (a quadrate) $Z_i = b(x_i, R_i)$ with the centre at a tree's cell x_i and a radius R_i. That is, a zone of nutrition consists of a square grid of cells with size 0.5 m × 0.5 m. The size of the grid expands to include more adjacent cells as the tree's diameter increases.

If there is no other tree overlapping a nutrition zone of the given tree x_i, then all available nitrogen within the zone is used for that tree's growth. In this case the total amount of available nitrogen taken up by the tree is the sum of available nitrogen over all cells belonging to the zone of nutrition. If the zone of tree x_i overlaps with the zone of another tree x_j, then the available nitrogen within the intersection zone has to be distributed between the competing trees.

If a cell falls in the zone of overlap, then the available nitrogen is distributed amongst the competing trees proportional to the biomass of their fine roots in this cell. We assume that fine roots are homogeneously distributed in the zone of nutrition of a tree. The amount of fine roots of the tree in a cell is calculated by dividing the total mass of fine roots of the tree by the number of cells that belong to its zone of nutrition. The amount of nitrogen (N_m) available to the tree is the sum of all the portions of available nitrogen in its area of nutrition.

2.1.5. Conversion of dendrometric characteristics into tree biomass to initialisation the model

Biomass of the leaves/needles and other tree compartments are the main variables of the tree model. We use standard inventory characteristics (height and diameter) to calculate the biomass of the tree compartments using species-specific regression equations (Marklund, 1988). In general, the form of the Marklund equation is

$$W_d = \exp\left(\frac{b_0 + b_1 D}{(D + g) + b_2 H + b_3 \ln H}\right) \tag{8}$$

where W_d is the dry weight of tree a compartment (kg), D is the diameter at breast height (DBH) (cm), H is the height (m) and $b_0, \ldots, b_3$ and g are species-specific coefficients. On the first initialisation step, the program generates the initial number of trees on a spatially explicit grid using height and diameters with their standard deviations.

2.1.6. Conversion of biomass increment back into diameter and height increment as in the original inventory characteristics

In the process of simulation, the model produces values of tree biomass compartments that should be converted back into standard dendrometric characteristics. We assume that tree volume can be described in terms of taper functions. In this case the stem biomass can be expressed as:

$$B_i = \rho_{\text{stem}}\left(\frac{\pi D^2}{12}\right)H, \tag{9}$$

where ρ_{stem} is wood density, initials D and H are known.

At next time step $(i+1)$

$$\frac{B_{i+1}}{B_i} = K, \quad H_{i+1} = k_{\text{h}}H, \quad D_{i+1} = k_{\text{d}}D, \tag{10}$$

where K, k_{h} and k_{d} are coefficients of stem biomass, H and D increase, and

$$B_{i+1} = \rho_{\text{stem}}\left(\frac{\pi k_{\text{d}}^2 D^2}{12}\right)k_{\text{h}}H. \tag{11}$$

From Eqs. (9)–(11) it is easily seen that

$$K = k_{\text{d}}^2 k_{\text{h}}. \tag{12}$$

In a case of a tapered stem shape,

$$k_{\text{d}} = k_{\text{h}} = K^{1/3}, \tag{13}$$

and finally

$$H_{i+1} = \left(\frac{B_{i+1}}{B_i}\right)^{1/3} H_i, \tag{14}$$

$$D_{i+1} = \left(\frac{B_{i+1}}{B_i}\right)^{1/3} D_i. \tag{15}$$

These equations are used in the model to calculate the diameter and height increment at any time step.

2.1.7. Reallocation of total biomass increment as adaptive procedure

2.1.7.1. Change of proportion between leaf/needle and fine root increment. If light is a limiting factor there can be excess unused available nitrogen. In this case, we assume that the tree's response results in an increase in leaf/needle biomass and a corresponding decrease in fine root biomass. We derived a simple system of equations to calculate the redistribution of increment between these two compartments while maintaining the total sum of nitrogen:

$$n_{\text{l}}\alpha_2 + n_{\text{fr}}\alpha_5 = K, \tag{16}$$

$$n_{\text{l}}(\alpha_2 + \delta) + n_{\text{fr}}(\alpha_5 - \delta) = K + \Delta N, \tag{17}$$

where K is a portion of available nitrogen going to leaf/needle and fine root increments, ΔN—excess of nitrogen, n_{l} and n_{fr}—SCN for leaves/needles and fine roots, respectively, and their corresponding proportions α_2 and α_5, and δ—the proportion of the gross increment going to needles/leaves. In order to maintain unity ($\sum \alpha_{\text{i}} = 1$), δ with the opposite sign is included in the expression for the proportion of fine roots. From the equations above it may be easily derived that

$$\delta = \frac{\Delta N}{(n_{\text{l}} - n_{\text{fr}})}. \tag{18}$$

There is a restriction that δ cannot be larger than $0.1\alpha_2$ to avoid unrealistic behaviour of the model.

2.1.7.2. Change of diameter/height ratio. We assume that when nitrogen is limiting, the tree allocates more of its increment to diameter than to height. For this purpose the following simple equations were derived.

In the case of the response to the light deficit

$$k_{\text{h}} = \beta_1 k_{\text{d}}, \tag{19}$$

$$K = k_{\text{d}}^2\beta_1 k_{\text{d}} = \beta_1 k_{\text{d}}^3, \tag{20}$$

and where $\beta_1 > 1$ is constant we have

$$k_{\text{d}} = \left(\frac{K}{\beta_1}\right)^{1/3}, \tag{21}$$

$$k_{\text{h}} = \beta_1 k_{\text{d}}. \tag{22}$$

In the case of nitrogen deficiency, we use the same expressions but with a different coefficient of $\beta_2 > 1$. Therefore, we have two driving coefficients to redistribute the stem's increment. Their values are close to 1 and can be calibrated against experimental data.

2.1.8. Tree mortality

A deterministic procedure of self-thinning is based on the idea of lethal threshold, defined by the ratio of leaf mass to total biomass, below which the tree dies. After the model calibration, we arrived at the following equation:

$$r = g_1 - g_2 \ln B_{\mathrm{T}}, \tag{23}$$

where r is the lethal ratio $B_{\mathrm{l}}/B_{\mathrm{T}}$ and g_1 and g_2 are species-specific parameters. The ratio is dependent on tree biomass, so the larger a tree is the lower the lethal ratio. The model is highly sensitive to changes of this parameter which strongly influences the rate of self-thinning. In additional, we inserted a probabilistic mortality function dependent on tree age that reaches 1.0 at a species-specific maximal tree age.

2.2. FGV—a ground vegetation dynamics submodel and a procedure for natural regeneration

The ground vegetation model FGV (Mikhailov, 2002) is represented as a dynamic model of a set of some functional plant groups. For an initial set we used typical boreal forest groups: mosses, sphagnum, herbs, grasses, blueberry (*Vaccinium myrtillus* L.) and clusterberry (*Vaccinium vitis-idaea* L.). The main equations used to describe the groups' biomass growth are similar to that in the submodel of EFIMOD 2 that calculates tree biomass. We assume that the potential for biomass growth increment is limited either by light or by available nitrogen following Liebig's law. The influence of water availability is accounted for by using a growth multiplier as in gap models (Chertov et al., 1999b). The model is realised as a system of balanced equations for biomass and element dynamics of functional plant groups competing for resources. Experimental data for the model compilation and testing is a set of previously published materials on ecological botany, forest science and biological productivity of different plant groups in Western Europe (mostly Finland and Sweden) and Russia. Natural regeneration may be included in this version of the model as a new forest cohort. Addition of the cohort may be customised to accommodate rules of planting or reproductive strategies characteristic of different species as described in the published literature.

The tree submodel (Section 2.1) and FGV submodel (this section) are joined with ROMUL—model of SOM dynamics (Chertov and Komarov, 1997; Chertov et al., 2001) and SCLISS the soil climate generator (Chertov et al., 2001; Bykhovets and Komarov, 2002) to create the forest ecosystem model EFIMOD 2.

2.3. ROMUL—a model of SOM dynamics

Litter cohorts with different chemical properties enter the soil (above and below ground) and are transformed into soil organic matter. SOM dynamics play a crucial role in the simulation of terrestrial ecosystem function since the soil processes of organic matter accumulation and decomposition are integral to nutrient supply, ecosystem stability and carbon balance in terrestrial ecosystems.

ROMUL (former SOMM, Chertov and Komarov, 1997), based on earlier simulations of forest floor mineralisation and humification (Chertov, 1985), has been developed using the classic pedological concept of "humus types". Each litter cohort is represented as one pool of litter fall and four of SOM: undecomposed litter, partly humified organic material in the organic layer (forest floor and peat), the same in the mineral topsoil (fraction of "labile humus") and stable humus bonded with the mineral matrix of the top soil. SOM humification is modelled as the consequence of a succession of processes regulated by three communities of saprophages. SOM mineralisation and nitrogen dynamics are simultaneously modelled for every pool along the successive stages of SOM decomposition.

The main features of the ROMUL model are as follows:

1. The main assumption is that there is a successional change in the complex of decomposer organisms that is correlated with the concepts of "raw humus", "moder" and "mull" genesis that exists in forest pedology (Wilde, 1958; Duchaufour, 1961).
2. The biomass of soil organisms represents a negligible part of all decomposed matter and has a high rate of decomposition; we do not take it into consideration as a separate pool.
3. It is well known that the number and species composition of decomposing organisms are dependent on the biochemical properties of the organic debris, hydrological and thermal conditions. We assume that there are no barriers for a rapid invasion of new organisms. Thus, it is possible to evaluate the decomposition coefficients for the communities as

a function of the biochemical properties of litter, temperature and moisture.

4. We divided the organic debris into two main groups: above-ground litter added on top of the soil surface where decomposition depends on the unique conditions of litter temperature and moisture, and below-ground litter consisting of root debris where decomposition depending on the unique conditions of soil temperature and moisture. The number of cohorts is not restricted.
5. The rate of the nutrients release due to mineralisation corresponds to the rate of the organic matter mineralisation. The only exception is nitrogen kinetics in the organic layers (forest floor and peat). Because of its high rate of consumption by soil microorganisms, the gross rate of nitrogen mineralisation is significantly lower than the rate of carbon mineralisation in the organic layers. In mineral horizons the rate of nitrogen release only corresponds to the rate of carbon mineralisation when the C/N ratio is less than 8 (Alexandrova, 1970). The dynamics of nitrogen have been described by Chertov (1985) and can be evaluated in ROMUL, including the evaluation of nitrogen available for plants (Chertov et al., 1999b,c).

Corresponding with these postulates, the kinetics of organic litter and humus transformation in the soil is expressed by a system of first order linear differential equations of with variable coefficients. The same system of equations has been written for nitrogen and other elements in the SOM. The values of the kinetic coefficients expressing the rate of SOM transformation to other fractions and its mineralisation depends on soil temperature, moisture, litter nitrogen and ash content.

The amounts of mineralised humus and nitrogen available for plants are important outputs from ROMUL and are calculated for every time step. The nitrogen available for plants is defined as the sum of mineralised nitrogen in different SOM fractions. Pools of organic matter and nitrogen in the SOM are expressed in kg m^{-2} for all soil horizons or layers with a fixed total thickness of 100 cm. Multiple litter fall cohorts are characterised by their ash and nitrogen content and location on (above-ground cohort) or in (below-ground cohort) the mineral soil. In the EFIMOD system, the litter cohorts that enter ROMUL are generated by tree and forest ground vegetation submodels. Climate data, such as air temperature, soil temperature at 20 cm depth, forest floor moisture and solum moisture, are necessary inputs to run ROMUL.

The iteration step in ROMUL is 1 day, but in the ecosystem model the input data are averaged monthly values. Model outputs include the simulated pools of L, F, H (organic matter and nitrogen), the C/N ratio of humus, gross production of carbon dioxide and available nitrogen due to organic matter mineralisation.

2.4. SCLISS—soil climate generator

A soil climate generator is used in the model for two purposes. First, as a method to estimate soil temperature and moisture using measured standard long-term meteorological data; and second, for statistical simulation (generation) of realisations of long-term series of necessary input climate data with known statistical properties for the Monte–Carlo procedure (Chertov et al., 2001; Bykhovets and Komarov, 2002). The generator was developed as a statistical one and is based on standard meteorological data with a monthly time step.

2.5. Additional procedures

Some additional parameters are included in the EFIMOD 2 system. They are: humus leached down H_{leach}, an annual input of atmospheric nitrogen N_{atm} (4 kg ha^{-1} in unpolluted conditions) and nitrogen leaching N_{leach}. The values for leaching in developed soils were calculated using published data (Kazimirov and Morozova, 1973) and a previous model developed by Chertov (1981):

$$H_{\text{leach}} = 0.0024 H_{\text{s}}, \tag{24}$$

$$N_{\text{leach}} = 0.0017 N_{\text{s}}, \tag{25}$$

where H_{s} is the total SOM mass in a soil ($H_{\text{s}} = L + F + H$) and N_{s} is the total nitrogen mass in the L and F soil compartments. H_{leach} is added to the equation for H in the main system of equations for ROMUL dynamics. N_{atm} is added to the litter nitrogen input, and N_{leach} is aggregated with forest floor nitrogen.

An important compartment of the nitrogen pool in the soil is nitrogen added by nitrogen-fixing microorganisms. This was calculated and added to the soil nitrogen using a previously developed formula (Chertov, 1981, p. 154).

$$N_{\mathrm{FIX}} = \frac{0.004}{N_L + N_F + N_H} - 0.0003 \quad (\mathrm{kg\,m^{-2}\ per\ year}), \qquad (26)$$

where N_L, N_F and N_H are nitrogen contents in *L*, *F* and *H* soil compartments, respectively.

2.6. Time step

The EFIMOD 2 system allows for model subsystems to operate on different time steps. The tree growth model uses the maximum possible annual increment to evaluate potential growth and therefore requires a yearly time step. The soil model operates with monthly steps taking into account seasonal temperature and precipitation effects and allows for the irregular arrival of litter. The forest ground vegetation model also operates on a monthly time step thus accommodating introduction of litter with seasonal variations.

2.7. Monte–Carlo procedure and the Forest Manager

Monte–Carlo procedures can be used to simulate the stochastic nature of external variables, such as random climatic inputs and uncertainties associated with the initial distribution pattern of trees, and the frequently unknown distributions for tree heights and diameters (only averages available in inventory data). These procedures are used in EFIMOD 2 to generate climate and soil inputs.

The individual-based spatially explicit structure of the tree model is ideally suited for the direct simulation of different kinds of cuttings practices. Therefore, the Forest Manager was developed to facilitate evaluation of the consequences of forest management practices on ecosystem properties. EFIMOD 2 has the potential to analyse the consequences of cuttings not only for the tree layer, but for the soil as well. The Forest Manager is not discussed in detail in this paper.

3. Sensitivity analysis of the model

3.1. Single tree growth

Simulations of an individual tree's response to different values of $\alpha_{\max}$ (grams of biological production per gram of leaves/needles per year) were done for a single tree growing in the open on different soils. We assumed that the mean area of tree nutrition is 25 $\mathrm{m^{-2}}$ and ran the simulation for 100 time steps on poor soil (SOM 2.4 $\mathrm{kg\,m^{-2}}$ and soil nitrogen 0.033 $\mathrm{kg\,m^{-2}}$), medium soil (12.6 and 0.32 $\mathrm{kg\,m^{-2}}$) and rich soil (19.3 and 0.50 $\mathrm{kg\,m^{-2}}$). Results for Scots pine, a shade-intolerant species and Norway spruce a shade-tolerant species, are shown in Fig. 3. A clear positive response to increasing $\alpha_{\max}$ was found for

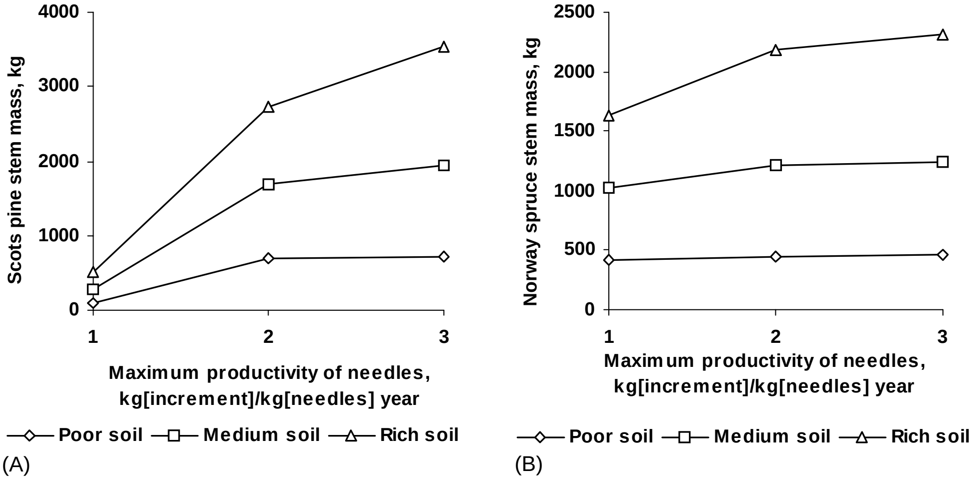

Fig. 3. (A) Scots pine response to different $\alpha_{\max}$ on soils of various productivity; (B) the same for Norway spruce.

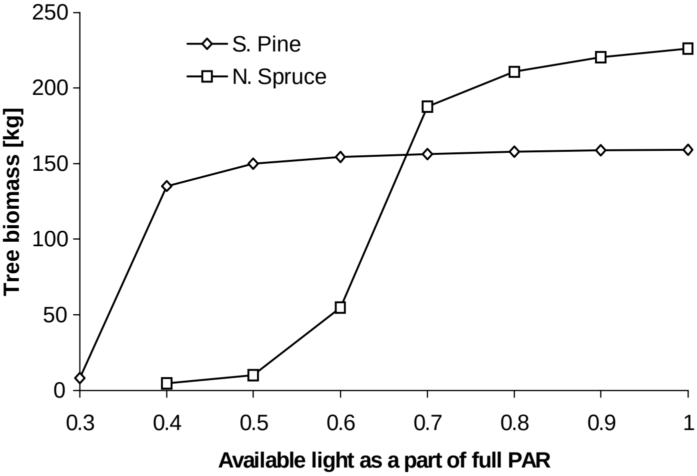

Fig. 4. Effect of shadowing (K_E reduction) on single tree growth (100 years simulation on very poor soil in North boreal zone).

both species on rich soils. The response is weak for poor soils. The effect of consistent decrease of light conditions due to shadowing (reduction of K_E value) of a single tree growing on poor soil conditions is shown in Fig. 4. The curves clearly express the different responses of shade-tolerant Norway spruce and shade-intolerant Scots pine to light reduction. Scots pine stops growth under light conditions where Norway spruce continues to grow.

The rules for tree increment partitioning amongst the tree compartments in the model are different for young, adult and old trees (Table 3). We tested the model's sensitivity to not changing the partitioning as the tree aged. The tree grows 10–20% slower if the partitioning for young and especially for old-aged trees is applied to the entire growth period, while tree biomass increased by about 30% biomass if grown with mean-aged status partitioning.

The process of nitrogen retention from senescent leaves is included in the model. This part of the leaves' nitrogen is withdrawn and stored in the tree to be used next Spring. The effects of varying the proportion of nitrogen retained and varying nitrogen response (SCN, N_T) on individual Norway spruce tree growth are shown in Fig. 5. The figure demonstrates that the physiological mechanism for nitrogen retention is effective if the tree has a high requirement for nitrogen, whereas it is not effective if tree has a low requirement for nitrogen, for growth. An important consequence of these relationships is that the greater the nitrogen retention from senescent leaves, the poorer the soil that develops under the stand.

We should also mention that the tree submodels show a high sensitivity to the adaptive procedures (Section 2.1.7) resulting in twofold changes of stem biomass, diameter and height.

3.2. Whole ecosystem dynamics

The model demonstrates a high sensitivity to tree nitrogen response if we vary the value of "specific consumption of nitrogen" as a tree ecological

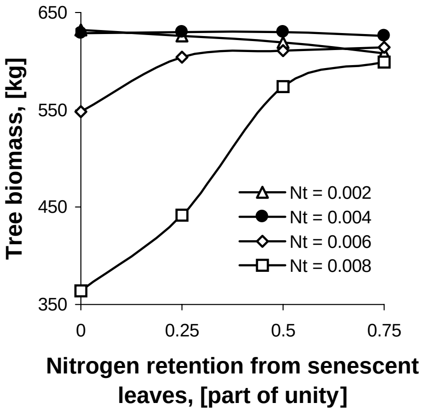

Fig. 5. Effects of a proportion of retained nitrogen on individual Norway spruce tree growth with variation of tree nitrogen response (specific consumption of nitrogen N_T).

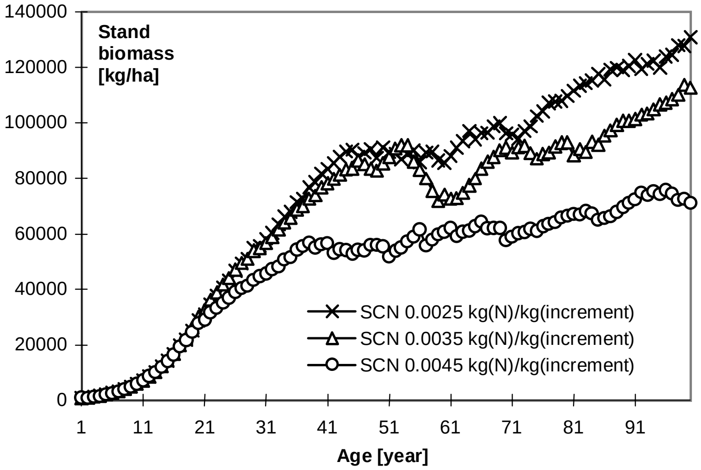

Fig. 6. The biomass dynamics of Scots pine stands on poor raw humus soils with variation of "specific consumption of nitrogen" (SCN).

characteristic. Experimental values of SCN for Scots pine and Norway spruce have been estimated as 0.0035 and 0.0044, respectively. Therefore, we tested the model's sensitivity to SCN by running simulations of Scots pine and Norway spruce stands on poor raw humus and rich moder–mull soils at SCN values of 0.0025, 0.0035 and 0.0045 $\mathrm{kg\,N\,kg^{-1}}$ increment per year for both tree species (Figs. 6 and 7). The lower the value of SCN (a) the higher the stand productivity (up to 2.5 times more in comparison with high SCN), (b) the weaker the stand self-thinning resulting in the formation of more dense stands, and (c) the higher the accumulation of nitrogen-poor raw humus on the soil surface. In the case of a high nitrogen response, the stands demonstrates slow growth but the ecosystem forms a rich soil with an accumulation of SOM in mineral topsoil. A high nitrogen content is associated with the moder–mull soils observed here with a C/N ratio 10.4–21.8 compared with 16.1–47.0 for the raw humus soils. Also, stand self-thinning starts

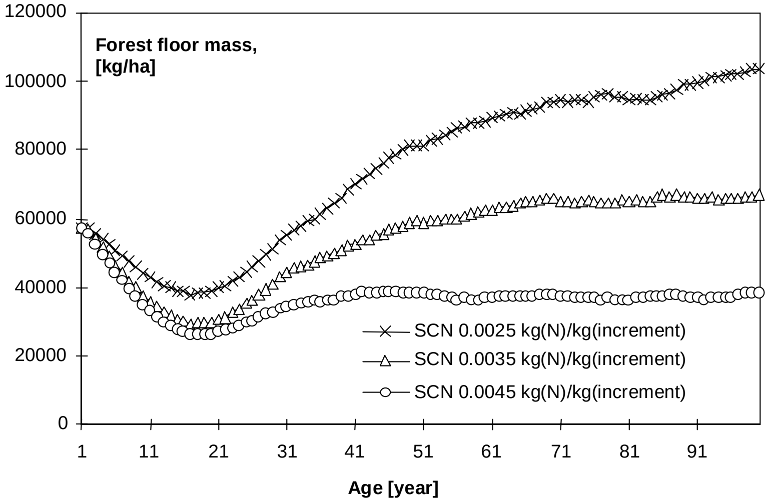

Fig. 7. The forest floor mass dynamics of Scots pine stands on poor raw humus soils with variation of "specific consumption of nitrogen" (SCN).

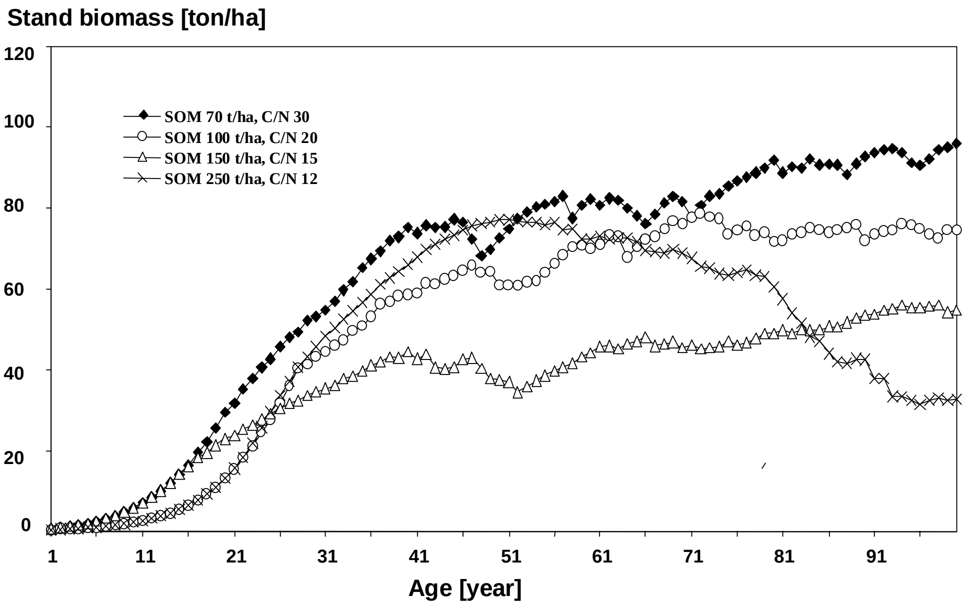

Fig. 8. Effects of soil organic matter and nitrogen increasing as a mull A1 on Scots pine biomass growth in North Taiga.

earlier and proceeds more intensely compared with the low values for SCN. The differences are more strongly expressed in the Scots pine ecosystems in a cold climate (annual temperature 1 °C) compared with Norway spruce ecosystems (annual temperature 4 °C) with initially rich soils in a warmer climate.

The simulation of pure Scots pine stands growth and soil development in the North boreal sub-zone (mean annual temperature 1 °C) with humus types ranging from raw humus to moder and mull soils showed growth decreasing with increasing SOM and nitrogen content in the A1 horizon as mull humus type (Fig. 8). However, the response of Scots pine stands showed the opposite with simulations over a range of soils with an increasing pool of SOM and nitrogen in the organic layer (forest floor and drained peat). The more productive stands have developed in association with the larger SOM pool (Fig. 9). These observations are consistent with observations in the North Taiga (Chertov, 1981; unpublished results). Conversely, the Silver birch stands demonstrated the "classical" response of trees to soil conditions. In the temperate climate of the South boreal zone both conifer and deciduous stands have the same "classical" response to soil conditions: on nitrogen-rich mull soils growth is significantly higher than on poor raw humus soils in all forests. These patterns of simulated growth sensitivity to various soils realistically reflects forest growth response to soil conditions in the Northern and Southern boreal zones reflecting the variable character of both forest–soil interactions and soil formation under coniferous and deciduous forests.

Simulation of Scots pine stands on different soils with an optimal moisture regime and varying mean annual temperature were performed to test the model's sensitivity to climatic conditions. The time series of stand biomass reflected the strong difference of growth rate in young stands. However, as the stands aged, growth slowed regardless of climatic conditions. This response also reflects reality: nutrient-poor soils strongly limit plant growth even under optimal conditions of temperature and precipitation. It is well known that severely damaged soils in all climatic zones cannot support self-sustaining growth, neither woody nor grass vegetation. Conversely, the stand growth on rich mull soils is strongly dependent on climate: the higher growth rate being correlated with a warmer climate.

Varying the parameters of the tree mortality function lead to significant changes in stands dynamics: the

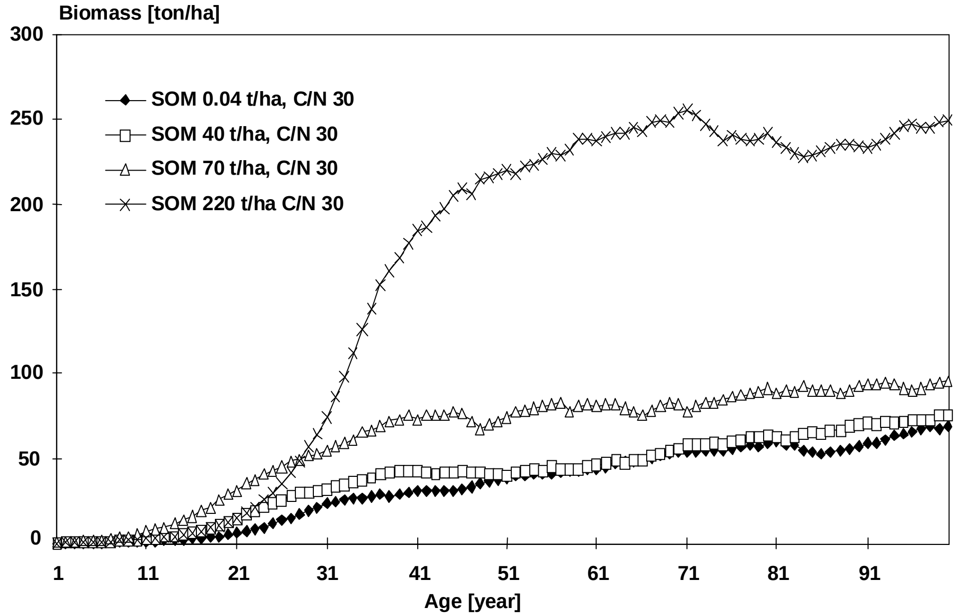

Fig. 9. Scots pine stand dynamics on raw humus and drained peat sites in North Taiga.

higher the mortality rate the stronger the self-thinning and the higher the mean tree diameter and height.

4. Discussion and conclusion

The tree submodel demonstrates a specific response to changes of $\alpha_{\max}$. It is sensitive on rich soils only. This reaction reflects the model's structure that uses Liebig's principle, which evaluates the relative influences of light conditions and available soil nitrogen on tree growth. On poor soil, the increment of the trees is limited by nitrogen deficit. In this case, the tree does not respond to the increasing values of potential NPP ($\alpha_{\max}$).

The tree submodels of different species displays the dissimilarity of growth under limited light reflecting their shade tolerance in the same manner as in the majority of gap models (Botkin et al., 1972; Ryan et al., 1996).

A new aspect of the proposed approach is the specification of some tree ecological parameters that depend on the tree's ontogenetic status. One example is biomass partitioning according to the age status. The tree model demonstrates considerable change in growth rate depending on the rules of biomass increment (NPP) partitioning between the tree compartments.

Nitrogen retention from senescent leaves exhibits a strong sensitivity and has significance for the whole ecosystem. The greater the nitrogen retention the greater the tree growth. However, the soil becomes poor and acts as an ecosystem feedback regulating tree growth.

The observed patterns of the whole model sensitivity emphasise the complex interactions of climate and soil as leading factors controlling stand growth. Firstly, tree ecological characteristics (SCN and reallocation of increment) strongly influence both stand growth and soil development. Secondly, in some cases there is a species-specific effect of the forest ecosystem on the soil condition, reflecting the close relationship between stand composition and soil properties formed by different tree species (Scots pine effect of increasing SOM accumulation in the organic layer in the North). Thirdly, poor soils limit stands from reaching their potential stand productivity ($\alpha_{\max}$) and ability to positively respond to a warmer climate.

Generally, we can conclude that the model is very sensitive to soil parameters and processes due to using

Liebig's "bottle-neck principle". In the model, the impact of temperature and precipitation is reflected only in the rate of soil processes and production of available nitrogen. Tree increment is calculating using the minimum value between the increment by fixed maximal parameter of NPP (reduced by shadowing) and, again, increment by soil nitrogen. Soil is the main driving factor in the EFIMOD 2 model. When absolutely identical initial parameters ($\alpha_{\max}$, reallocation and nitrogen retention, SCN, stand and soil parameters) are used but with different climates (Skogaby (South Sweden), mean annual air temperature 7 °C, and St. Petersburg (Northwest Russia), mean annual air temperature 4 °C) that determine different parameters of soil temperature and moisture, strong differences in stand growth are observed (Fig. 10). We do not think that this specific feature of the model is a drawback. On the contrary, it is the advantage of the model, because the soil is mostly a passive compartment in the majority of other forest simulation models, and the feedbacks in the "stand–soil" system are rarely discussed (Chertov et al., 1999a).

The fitness of the model should also be checked using independent experimental data. We performed such a comprehensive model validation, and it will be described as a separate paper.

Consider one more important feature of the main model's structure. Pacala and Deutschman (1995) showed that individual-based models might have a different dynamics compared with traditional gap or cohort models. The following model experiment illustrates how the EFIMOD 2 system expresses such a difference.

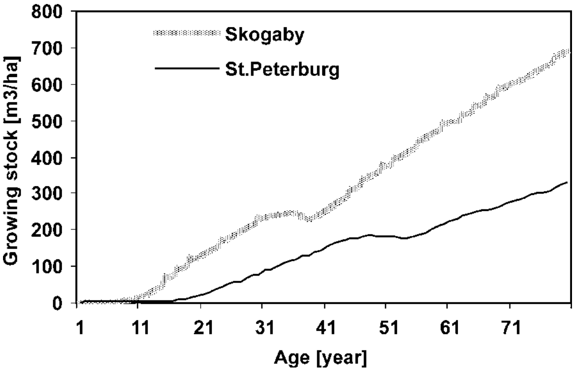

Fig. 10. Climatic response of the model (see the text).

Remember that nutrition zones of different trees may overlap and that the redistribution of available nitrogen from the overlapping nutrition zones may be defined in different ways. If there is no other tree, overlapping a nutrition zone of the given tree x_i, then all available nitrogen within the zone is used for nutrition of this plant. In this case, the total amount of available nitrogen going to the tree is the sum of available nitrogen over all cells belonging to the zone of nutrition. On the other hand, if the zone of tree x_i overlaps with the zone of another tree x_j, rules have to be defined for the distribution of the available nitrogen from the cell to different trees. We compared the effect of two different rules on the stand densities of birch and spruce.

The first rule (global rule) is to distribute the available nitrogen proportionally to the of the trees' total fine root biomass. In this case a tree consumes nitrogen from an intersection zone of several trees proportional to its own fine root biomass. This rule originates from cohort models.

The second rule (local rule) is to distribute the available nitrogen proportionally to the biomass of fine roots of the trees in each cell. We assume that fine roots are homogeneously distributed in the zone of nutrition. The amount of fine roots belonging to a tree in a cell are calculated by dividing the total mass of fine roots by the number of cells belonging to the zone of nutrition of that tree.

Initial data for the run were defined as follows: soil L (undecomposed litter) $= 0.5\,\mathrm{kg\,m^{-2}}$; nitrogen in $L = 0.03\,\mathrm{kg\,m^{-2}}$; F (humified organic layer) $= 3.1\,\mathrm{kg\,m^{-2}}$; nitrogen in $F = 0.068\,\mathrm{kg\,m^{-2}}$; H (SOM in mineral topsoil) $= 10.6\,\mathrm{kg\,m^{-2}}$; nitrogen in soil $= 0.245\,\mathrm{kg\,m^{-2}}$. This is birch MT type in the Finnish soil classification system. The initial values for the stands are for spruce: 10 years old, average height 1.0 m, S.D. 0.1 m; average diameter at 1.3 m (DBH) is 0, S.D. is 0; and for birch: 10 years old, average height 1.8 m, S.D. 0.1 m, DBH is 0.5 cm, S.D. 0.1 cm.

It is clear that the dynamics of each species are strongly dependent on the rule used for distribution of soil nitrogen (Fig. 11). Using the "global rule" spruce stand density declines but with the "local rule" it is the birch stand density that declines. The explanation is simple but not obvious. Since birch is faster growing than spruce it expands its zone of nutrition at a faster rate. When the competition (i.e. overlapping zones of nutrition with small spruce trees) occurs under the

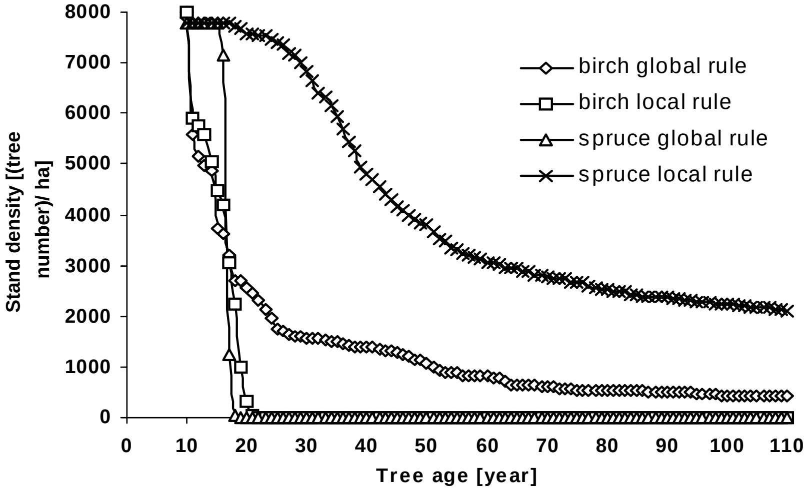

Fig. 11. Mixed stand dynamics at different rules of distribution of soil available nitrogen among trees (see the text).

"global rule" birch is allocated more available nitrogen from a competing cell due to its large size. Using the "local rule" the relative portion of birch fine roots is small while the concentration of spruce fine roots in a cell from a small zone of nutrition is high. Thus, it can be seen that EFIMOD 2, with the capability of applying the "local rule", is able to reflect the significant effect of competition between species with different rate of growth in young-aged stands.

It should be noted that the main sources of uncertainties for the model's application are the initial data and rules for distribution of annual increment. It was shown in Fig. 11 that the rules of distribution are very important for the growth of individual trees. It is difficult to find appropriate experimental data for the calibration of these rules. Moreover, splitting the tree ontogenesis into three stages might be not enough. Perhaps, splitting ontogenesis into more short ontogenetic stages is more appropriate (Chertov et al., 1999a; Smirnova et al., 1999). However, availability of the necessary experimental data is still in question.

Another source of uncertainty is the initial soil data. It is impossible to have all of these variables well measured, some will always be estimated. The EFIMOD 2 model runs show that the values of the most important variables for elements turnover, such as available nitrogen, are mostly provided by litter flow. The initial soil data come into balance with litter flow quickly and the initial uncertainty fades away. One possible means to account for the errors in evaluation of initial data is an application of Monte–Carlo procedure in relation to soil input data. The Monte–Carlo analysis can also evaluate the significance of climate input.

The results of the EFIMOD 2 model analyses shows that it can be applied successfully to assess forest ecosystem function and nutrient dynamics and forest ecosystem response to climate change, natural disturbance agents (fire and insects) and forest management practices.

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