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A simulation model for the succession of the boreal forest ecosystem

Seppo Kellomäki, Hannu Väisänen, Heikki Hänninen, Taneli Kolström, Risto Lauhanen, Ulla Mattila & Brita Pajari

TIIVISTELMÄ: POHJOISEN HAVUMETSÄN SUKKESSIOTA KUVAAVA SIMULOINTIMALLI

Kellomäki, S., Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U. & Pajari, B. 1992. A simulation model for the succession of the boreal forest ecosystem. Tiivistelmä: Pohjoisen havumetsän sukkessiota kuvaava simulointimalli. Silva Fennica 26(1): 1–18.

A model for the succession of the forest ecosystem is described. The growth and development of trees and ground cover are controlled by temperature and light conditions and the availability of nitrogen and water. In addition, the effects of the annual cycle of trees including the risk of frost damage, wild fire, and windblow are contained in the model as factors which control the survival and productivity of trees. The model also makes it possible to evaluate the risk of insect attack assuming that this risk is inversely related to the growth efficiency of trees.

Julkaisussa kuvataan typen kiertoon perustuva metsäekosysteemimalli, jossa myös lämpöolosuhteet sekä valon ja veden saatavuus vaikuttavat puuston ja pintakasvillisuuden kasvuun ja kehitykseen. Malliin voidaan sisällyttää myös puiden vuotuinen sykli, jolloin voidaan tutkia puiden vuotuisen syklin ja vuotuisen lämpötilasyklin synkronoitumista ja vaikutusta puiden kasvuun ja kehitykseen. Malliin sisältyy vaihtoehtoisina prosesseina myös pakkasvaurioiden, metsäpalon ja myrskytuhon mahdollisuudet, jolloin näiden luontaisten häiriötekijöiden vaikutuksia metsäekosysteemin sukkessioon on mahdollista tarkastella. Myös hyönteistuhojen riskiä ja hyönteistuhojen vaikutusta puiden kasvuun ja tuotokseen voidaan arvioida olettamalla, että hyönteistuhojen riski on kääntäen verrannollinen puiden kasvutehokkuuteen.

Keywords: forest ecology, ecosystems, succession, simulation models, gap dynamics.
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1 Introduction

The dynamics of the boreal forest is controlled by several endogenic and exogenic factors. For example, the regeneration, growth, and death processes outline the succession of the tree community. This pattern could be modified, for example, by fires and storms, and even severe summer frosts (Sakai and Larcher 1987). Such external disturbances drive the succession when creating space for new seedlings to root and grow. The importance of external disturbances in driving the dynamics of the boreal forest ecosystem is widely accepted and applied in managing forest resources (Sernander 1936, Kuusela 1990).

The successional processes in boreal conditions create a forest structure characterized by gap-phase dynamics, i.e., succession is only re-started by the creation of gaps habitable for one or several tree species. The succession is directional from shade-tolerant species towards more shade-tolerant species, until external disturbance intervenes (Leemans and Collins 1989). This pattern has been widely used (Shugart and West 1977, El-Bayoumi et al. 1984, Kercher and Axelrod 1984a, b) in modelling the dynamics of a tree stand since Botkin et al. (1972) introduced the Jabowa model for describing the compe-titional process in multi-species tree communi-ties.

Gap-models simulate the dynamics of a tree population in a patch of forest land allowing trees to regenerate, grow, and die under the interaction between the tree community and its physical environment. If the size of the patch equals the maximum crown area of the largest trees, a single tree can dominate the patch. The death of this tree marks the onset of the succes-sion, which is thus characterized by a series of patches at different phases of development (Watt 1947, Shugart 1984). The same principle can be applied if the patch size exceeds the maximum crown area of the largest trees, which is common in boreal conditions (Leemans and Collins 1989).

The present paper describes a simulation mod-el for the succession of the boreal forest ecosys-tem based on the model by Pastor and Post (1985, 1986). The present model includes light, soil water, nitrogen, temperature, and sub-zero temperatures as factors controlling the birth, growth, and death of trees. In addition, the effect of wild fire and windblow are introduced in the model ecosystem. While the model is only out-lined here, the major modifications in the origi-nal model are described.

2 Model structure

2.1 Dynamics of tree stand

The dynamics of the forest ecosystem is as-sumed to be determined by the dynamics of the number and mass of trees as controlled by the birth, growth, and death of trees. All these proc-esses are related to the availability of resources as controlled by the dynamics of the gaps in the canopy of the tree stand. The same is assumed to apply to the ground cover species.

The dynamic equation for the *number* (NM_i, i = species) of individuals of each species can be written using the principle that the net growth of tree number in the year t equals the gross growth of tree number (B) minus the mortality of trees (D)

$$NM_i(t) = NM_i(t-1) + B_i(t) - D_i(t) \qquad (2.1)$$

The dynamic equations for the *mass* of a stand can also be written using the above principle, i.e., that the net growth of each component of any tree in the year t equals the gross growth of that tree component minus the senescence of the same component. Thus,

$$N_i(t) = N_i(t-1) + GN_i(t) - DN_i(t) \qquad (2.2)$$

$$BR_i(t) = BR_i(t+1) + GBR_i(t) - DBR_i(t) \qquad (2.3)$$

$$S_i(t) = S_i(t-1) + GS_i(t) - DS_i(t) \qquad (2.4)$$

$$R_i(t) = R_i(t-1) + GR_i(t) - DR_i(t) \qquad (2.5)$$

where N indicates the foliage, BR branch, S stem and R root, and G and D growth and death, respectively.

2.2 Dynamics of environment

The *light* conditions in a stand is controlled by the dynamics of gaps, which is determined the number and properties of trees in a stand. *Tem-perature* and *precipitation* vary on a monthly (k) basis in accordance with the annual weather pattern. Precipitation (PRECIP), evaporation (EVAP), and runoff (RUNOFF) determine the dynamics of the *soil water* (ASW)

$$ASW(k) = ASW(k-1) + PRECIP(k) - EVAP(k) - RUNOFF(k) \qquad (2.6)$$

The dynamics of available *nitrogen* (AVAILN) is determined by the nitrogen released (TMIN) in decomposition of organic matter in soil, de-posited from the atmosphere (NDEPOS), im-mobilized (TNIMOB) in the decomposition of organic matter in soil and wash-away (NWASH) from the site, i.e.,

$$AVAILN(t) = AVAILN(t-1) + TMIN(t) + NDEPOS(t) - TNIMOB(t) - NWASH(t) \qquad (2.7)$$

Organic matter (ORGM) in soil is treated by cohorts, i.e.,

$$ORGM(t) = ORGM(t-1) + LITTER(t) - DECOMP(t) \qquad (2.8)$$

where LITTER indicates litter and DECOMP the organic matter decomposed. Let NORGM indicate the nitrogen bound in organic matter in growth. Consequently,

$$NORGM(t) = n(t-j) \cdot ORGM(t-j) + ... + n(t) \cdot ORGM(t) \qquad (2.9)$$

$$TMIN(t) = dec(t-j) \cdot NORGM(t-j) + ... + dec(t) \cdot NORGM(t) \qquad (2.10)$$

$$TNIMOB(t) = imm(t-j) \cdot NORG(t-j) + ... + imm(t) \cdot NORGM(t) \qquad (2.11)$$

$$NWASH(t) = constant \qquad (2.12)$$

$$NDEPOS(t) = constant \qquad (2.13)$$

where n indicates the nitrogen concentration of organic matter (%), dec the decomposition rate (%) and imm the immobilization rate (%) and j the cohort of organic matter. The rate of de-composition and immobilization are assumed to be related to the quality of organic matter (e.g. carbon, lignin, nitrogen).

3 Implementation

3.1 Outlines

The above conceptual model for the dynamics of the forest ecosystem is substantiated by the algorithm which incorporates the subroutines for temperature, moisture, frost, and decompo-sition. These subroutines are linked by the mul-tipliers to the demographic subroutines (birth, growth, kill), which compute the population dy-namics. The effect of wild fire and windblow is introduced through the subroutine for kill, which affects the risk of a tree dying at a given moment. The site conditions and the risk of wild fire and windblow determine the birth, growth, and death of individual trees. Each time such an event is possible, the algorithm determines whether or not the event will be realized by comparing a random number with the probability of the oc-currence of the event (Monte Carlo technique). The probability of the event is a function of the state of the forest ecosystem at the time it is possible. Each model run is one realization of all possible time courses for the forest ecosys-tem. Therefore the simulation must be repeated several times to determine the central tendency or variations in the time behavior of the model ecosystem (Fig. 1).

3.2 Temperature and precipitation

The *precipitation* and *temperature* data are given as the monthly means and their standard deviations. Precipitation is treated as in the original model. Temperature acts on the annual and daily bases depending on the process. On the *annual* basis the temperature used is the temperature sum calculated from the mean monthly temperatures where the year-to-year pattern is calculated as a random temperature (RT(k)) normally distributed around the mean temperature (T(k)) for the month k
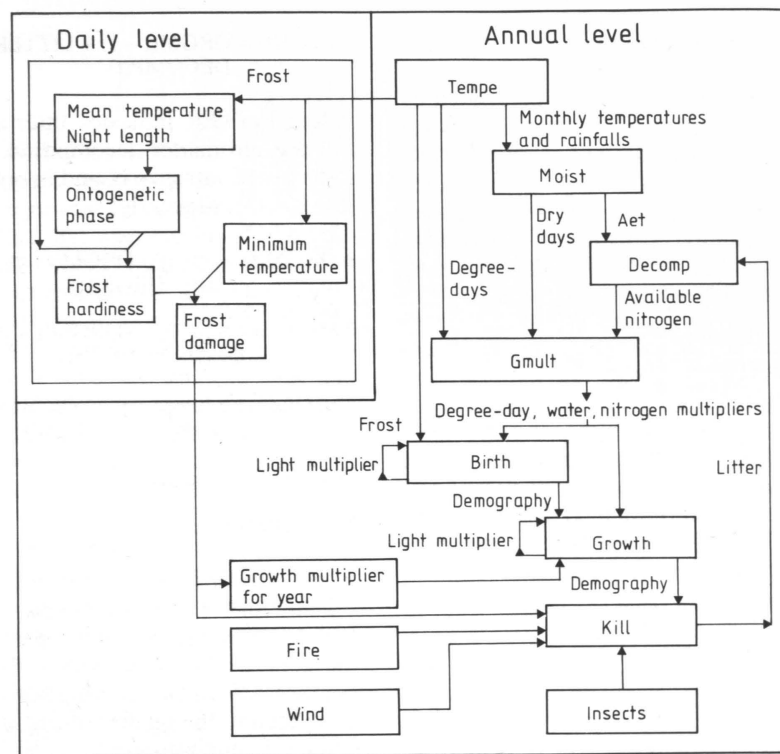
$$RT(k) = T(k) + VT(k) \cdot Z(k) \qquad (3.1)$$

Fig. 1. Outlines of the model.

Fig. 2. Outlines of the calculation of decomposition of litter and humus and mineralization of nitrogen.

where $Z(k)$ is the random number and $VT(k)$ the standard deviation of the mean temperature for a given month. The number of degree days (DEGR) [d.d.] for a year is

$$\text{DEGR} = \sum_{i=1}^{12} \max\{0, RT(k) - 5°C\} \cdot \overset{©}{\text{DAYS}}(k) \quad (3.2)$$

where 5 °C is the base temperature above which degree days are counted and $DAYS(k)$ is the number of days in a given month.

The simulation of the ontogenic development of trees requires the temperature condition on a *daily* basis. This is calculated by a random procedure which determines the daily mean and minimum temperatures in such a way that the mean monthly temperatures and their standard deviations are realized in each month

$$MEAN(i) = RT(k) + VT(k) \cdot Z(i) \quad (3.3)$$

$$TMINI(i) = A \cdot RT(k) + B \quad (3.4)$$

where $MEAN(i)$ is the mean temperature and $TMINI(i)$ the minimum temperature for the i:th day from the beginning of the year, and A and B parameters having the values $A = 0.967887$ and $B = -4.406415$ as estimated iteratively to suffice the above criteria regarding the mean monthly temperatures and their standard deviations.

3.3 Soil moisture

The availability of soil moisture is indicated by the number of dry days in the growing season as in the original model. The concept of dry day indicates a day with inadequate soil moisture for tree growth. The initial value of soil water in each year equals the field capacity of the soil. Thereafter the monthly potential evapotranspiration is calculated using the method described by Pastor and Post (1985). If the monthly evaporative water loss is greater than the monthly precipitation, the water loss is supplied from the soil water. When the monthly evaporative loss is less than the precipitation, the excess water is added to the soil water, if the amount of w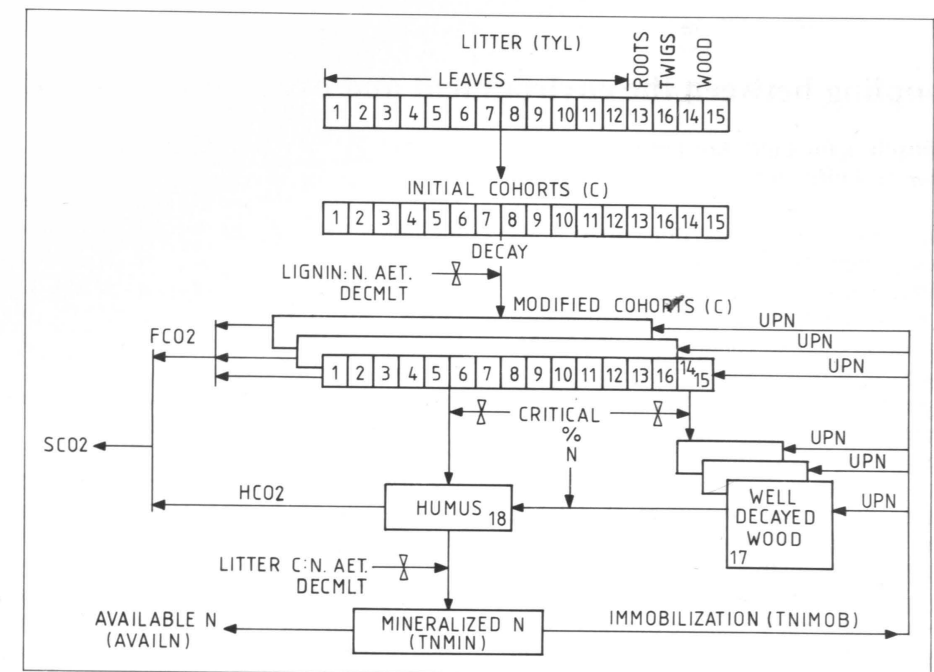ater is less than determined by the field capacity; it is assumed to run off if the amount of water is greater than determined by the field capacity. Any day is a dry day, if the amount of soil water is less than that determined by the wilting point. The calculation only concerns the days of the growing season.

3.4 Soil nitrogen

The decomposition of litter and humus is applied as in the original model. The decomposition of *litter* is used to calculate the weight loss, nitrogen immobilization, lignin decay, and carbon dioxide loss from decomposing litter cohorts. The weight loss of litter is a function of the current ratio between lignin and nitrogen. Whenever the nitrogen concentration of the decaying litter exceeds the critical concentration (a parameter), the organic matter and nitrogen of the litter cohort are transferred to the organic matter and nitrogen of the humus. The amount of nitrogen immobilized in decay is linearly related to the amount of nitrogen immobilized per unit weight loss (Fig. 2).

The decomposition of *humus* is used to calculate nitrogen mineralization, weight loss of humus, and carbon dioxide loss from humus. The mineralization of nitrogen is a function of the humus weight and the quality of humus (nitrogen/carbon-ratio) and the prevailing temperature and water conditions. The total nitrogen *available* for trees and ground vegetation is obtained by subtracting the immobilized nitrogen from the total mineralized nitrogen and adding the nitrogen deposited. The amount of nitrogen bound in the biomass is linearly related to the total accumulation of mass in the plant cover. The wash-away of nitrogen is not considered in the present algorithm.

4 Coupling between the environment and dynamics of tree stand

4.1 Multipliers for light, temperature, soil water and nitrogen

The coupling between the environment and the dynamics of tree stand is based on the *growth multipliers*, e.g. $G = G_o \cdot M_1...M_n$, where G is growth and/or regeneration, G_o growth and/or regeneration in optimal conditions and $M_1...M_n$ multipliers for different environmental factors. In the present model the multipliers for light, temperature, water, and nitrogen are used as in the original model. Therefore only the basic equations of these multipliers given (Table 1). For further details, see Botkin et al. (1972), Aber and Melillo (1982), and Pastor and Post (1985, 1986). The textbook by Shugart (1984) is also recommended for further details concerning the background of these multipliers. In addition, a multiplier for frost damage is included in the present model as described below.

4.2 Multiplier for frost damage

Phase of the annual ontogenetic cycle. The multiplier for frost damage includes the effects of the annual ontogenetic development (Sarvas 1972, 1974, Koski and Sievänen 1985, Hänninen 1990a,b, Hänninen et al. 1990) and frost hardiness of the trees (Repo et al. 1990) as well as the consequent effect on the regeneration, growth, and death of trees. Four developmental phases are distinguished by four distinct developmental events. The model combines the timing of each of the developmental events for the whole cycle. Daily mean temperature and night length are the inputs in the calculations (Fig. 3).

Trees have no growth competence during the lignification phase and rest phase. Starting annually on the day after growth cessation, the development of trees is simulated by accumulating a *lignification* temperature sum TS_{lgn} (day

Table 1. Functions and explanations for the growth multipliers.

Multiplier for light (Y_I)

$Y_I = A1 \cdot (1 - \exp(A2 \cdot (AL - A3)))$,

AL = exp(SL/SLEAFA), AL the share of light [0...1], SL the amount of foliage [kg/ha], SLEAFA a parameter [ha/kg] and A1, A2 and A3 parameters [dimensionless].

Multiplier for temperature (Y_T)

$Y_T = 4 \cdot (Dmax - X) \cdot (X - Dmin)/(Dmax - Dmin)^2$,

Dmin is the minimum value of the temperature sum [d.d., threshold 5 °C], Dmax the maximum value of the temperature sum [d.d.] permitting a particular tree species to survive and X the temperature sum [d.d.].

Multiplier for soil water (Y_W)

$Y_W = ((D_3 \cdot TGS - Fj)/D_3 \cdot TGS))^{0.5}$

TGS is the total length of the growing season in days, D_3 the maximum proportion of the total length of the growing season for a species to tolerate soil moisture below the wilting point, and Fj the percentage of dry days in the total number days of the growing season.

Multiplier for soil nitrogen (Y_N)

$Y_N = (N4 + N5 \cdot CONN)/1.7$,

where CONN = $N1 \cdot (1 - 10^{N2}(-170 + 4000 \cdot (AVAILN) + N3)))$, N4 [dimensionless], and N5 [%$^{-1}$] are parameters and CONN the nitrogen concentration of foliage [%], N1 [dimensionless], N2 [ha/kg], and N3 [kg/ha] parameters and AVAILN the amount of nitrogen available for growth [kg/ha].
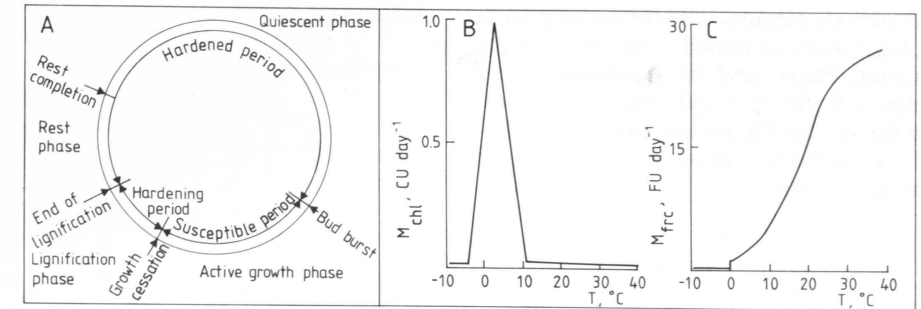

Fig. 3. (A) ontogenetic events and phases, and frost hardiness periods in the annual cycle of the development of trees, and temperature responses of (B) rate of chilling, M_{chl}, and (C) rate of forcing, M_{frc}, in the model for rest completion and bud burst. CU (chilling unit) and FU (forcing unit) are arbitrary developmental units for rest break and ontogenetic development, respectively.

°C, threshold temperature +5 °C). The end of lignification is attained whenever TS_{lgn} exceeds the critical value TS_{crit}.

Rest is broken as a result of chilling occurring after the end of lignification. Starting annually on the day after the end of lignification, the rate of chilling M_{chl} is

$$M_{chl(i)} = \begin{cases} 0, & \text{if } T(i) \leq -3.4°C \quad (4.1) \\ a_1 \cdot T(i) + a_2, & \text{if } -3.4°C < T(i) \leq 3.5°C \\ a_3 \cdot T(i) + a_4, & \text{if } 3.5°C < T(i) \leq 10.4°C \\ 0, & \text{if } T(i) > 10.4°C \end{cases}$$

where T(i) is the prevailing air temperature, a_1 = 0.159 CU day^{-1} °C^{-1}, a_2 = 0.506 CU day^{-1}, a_3 = −0.159 CU day^{-1} °C^{-1}, and a_4 = 1.621 CU day^{-1}. State of *chilling* at a given day i, $S_{chl}(i)$, is calculated by integrating rate of chilling, M_{chl}, from the end of lignification to the day i. Rest completion takes place if S_{chl} exceeds the critical value CU_{crit}.

During the *quiescent* phase trees have growth competence, but remain dormant due to the low air temperature. Ontogenetic development towards bud burst takes place as a result of exposure to forcing temperatures (T > 0 °C). Starting annually on the day after rest completion, rate of forcing M_{frc} is

$$M_{frc(i)} = \begin{cases} 0, & \text{if } T(i) \leq 0°C \\ \dfrac{a_5}{1 + e^{a_6 \cdot (T(i) - a_7)}}, & \text{if } T(i) > 0°C \end{cases} \quad (4.2)$$

where T(i) is the prevailing air temperature, a_5 = 28.4 FU day^{-1}, a_6 = −0.185 °C^{-1}, and a_7 = 18.4 °C.

State of forcing at a given day i, $S_{frc}(i)$, is calculated by integrating rate of forcing M_{frc} from rest completion up to the day i. Bud burst takes place, when S_{frc} attains a critical value FU_{crit} (forcing requirement of bud burst).

Timing of growth *cessation* is regulated by the interaction of night length and air temperature. The value of the regulating joint factor JF at a given time moment i is

$$JF(i) = NL(i) + a_8 \cdot TS_{grw}(i) \quad (4.3)$$

where NL(i) is prevailing night length in hours, $TS_{grw}(i)$ the prevailing value of a temperature sum calculated from the day after bud burst (day °C, threshold temperature +5 °C), and a_8 = 0.0088 h d.d.$^{-1}$. Growth cessation takes place on the first day, when JF(i) ≥ JF_{crit} (joint factor requirement of growth cessation), and $TS_{grw}(i) \geq TS_{min}$.

Annual course of frost hardiness. It is assumed that a stationary frost hardiness, H_{str}, is attained in any constant temperature, that the value of H_{str} depends linearly on prevailing temperature, and that the rate of change in actual hardiness H increases with the growing difference between the actual hardiness and stationary hardiness H_{str} (Repo et al. 1990). This approach is otherwise applied in the frost hardiness model of the present study, but the phase of the annual ontogenetic cycle is taken into account in the present model in the calculation of the stationary frost hardiness.

The annual cycle is divided into three periods of frost hardiness, and the calculation of H_{str} is determined for the prevailing period. The *sus-*

ceptible period coincides with the active growth phase, the *hardening* period coincides with the lignification phase, and the *hardened* period coincides with the rest and quiescent phases. During the susceptible period, trees have minimum frost hardiness and no potential for frost hardening, i.e., stationary frost hardiness is a constant (H_1)

$$H_{str}(i) = H_1 \tag{4.4}$$

During the hardening period, frost hardiness increases with night length (Fuchigami et al. 1982). During this period, H_{str} is (Fig. 4)

$$H_{str(i)} = \begin{cases} H_1, & \text{if } NL(i) \leq NL_1 \\ \dfrac{H_2 - H_1}{(NL_2 - NL_1)} \cdot (NL(i) - NL_1) + H_1, & \text{if } NL_1 < NL(i) \leq NL_2 \\ H_2, & \text{if } NL(i) > NL_2 \end{cases} \tag{4.5}$$

where $NL(i)$ is the prevailing light length, NL_1 and NL_2 threshold values of night length, and H_1 and H_2 values of stationary frost hardiness in night lengths below NL_1 and above NL_2, respectively.

During the hardening period, frost hardiness fluctuates according to air temperature (Repo et al. 1990). During this period, H_{str} is

$$ \tag{4.6}$$

$$H_{str(i)} = \begin{cases} H_4, & \text{if } T(i) \leq T_1 \\ \dfrac{H_3 - H_4}{(T_2 - T_1)} \cdot (T(i) - T_1) + H_4, & \text{if } T_1 < T(i) \leq T_2 \\ H_3, & \text{if } T(i) > T_2 \end{cases}$$

where $T(i)$ is the prevailing air temperature, T_1 and T_2 the threshold values of air temperature,

and H_3 and H_4 the values of stationary frost hardiness obtained in temperatures above T_2 and below T_1, respectively (Fig. 4).

Rate of change in frost hardiness, $dH(i)/di$, is calculated during each of the three periods as follows

$$\frac{dH(i)}{di} = \frac{1}{\tau} \cdot ((H_{str}(i) - H(i)) \tag{4.7}$$

where τ is the time constant for attaining the stationary frost hardiness, H_{str} the stationary frost hardiness, and $H(i)$ the actual frost hardiness. Actual frost hardiness at a given moment, $H(i)$, is obtained by integrating Eq. (4.7) up to the moment i.

Annual frost damage. Frost damages were assessed by comparing the values of actual frost hardiness, $H(i)$, and minimum air temperature, $T_{min}(i)$, with the relative effect of frost damage on the growth (GF(i)) equation (Fig. 5)

$$GF(i) = \frac{1}{1 + \exp(b \cdot (H(i) - T_{min}(i)))} \tag{4.8}$$

where b is the slope parameter determining the width of the temperature range in which frost damage increases from negligible (e.g. GF(i) > 0.9) to full damage (e.g. GF(i) < 0.1). The temperature range is narrow during the susceptible period, intermediate during the hardening period, and wide during the hardened period.

Two different effects of frost damage on trees are taken into account in the model. *First*, the chronic growth-reducing effect of frost is determined by calculating the annual mean growth multiplier Y_c over the year

$$Y_c = \frac{1}{365} \cdot \sum_{1}^{365} GF(i) di \tag{4.9}$$
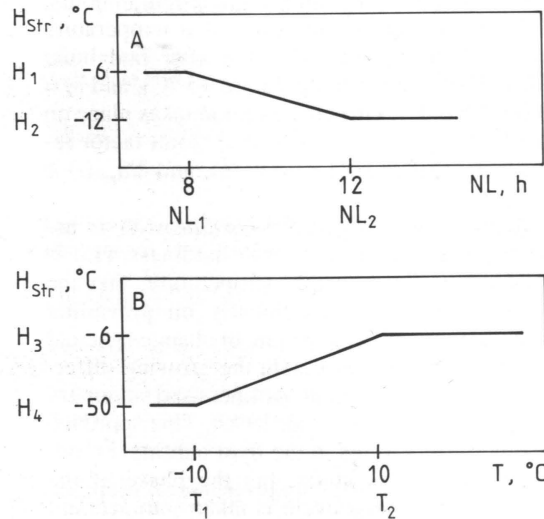
Fig. 4. Dependence of stationary frost hardiness, H_{str}, (A) on night length NL during hardening period, and (B) on air temperature T during hardened period. Figures on the axis indicate the suggested parameter values to be used in the simulations.

The multiplier Y_c is used in the succession model at the annual level, low values of Y_c reducing the rate of growth and increasing the risk of a tree dying in the succession model (see Fig. 2.1). *Second*, the killing effect of frost is described by removing the tree from the population, if GF(i) < 0.1 during any time of the year.
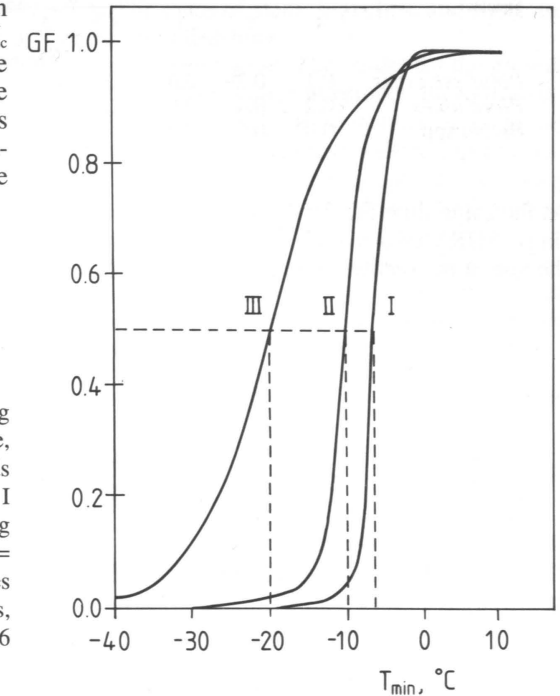
Fig. 5. Dependence of the relative growth-reducing effect of frost, GF, on minimum temperature, T_{min}, during three frost hardiness periods. Periods and corresponding values of slope parameter b: I = susceptible period (b = 0.8), II = hardening period (b = 0.6), and III = hardened period (b = 0.2). During each phase, the location of the curves shifts according to the prevailing frost hardiness, H. The three curves illustrate cases where H = –6 °C, H = –10 °C, and H = –20 °C, respectively.

5 Calculation of dynamics of tree stand

5.1 Regeneration

The subroutine for birth allows the regeneration of a tree stand naturally through seeding and/or sprouting or artificially through planting as in the original model, but the subroutine is thoroughly revised in regard to the development of seedlings (age < 12 years) (Fig. 6). *Seeding* is possible only for those species whose light requirements, drought tolerance, and frost tolerance are satisfied on the forest floor. *Sprouting* is possible if the light on the forest floor is at least 50% of that above the canopy, and the species is capable of sprouting in these conditions.

The seedlings (NPLANT, stems/ha) and sprouts (SPLANT, stems/ha) born in a particular year form a cohort. The total size of a cohort (TPLANT) equals the potential number of offspring due to seeding and sprouting. The potential number of offsprings (TPLANT = NPLANT + SPLANT) is reduced by the growth multipliers

$$NPLANT = SEEDMX \cdot Y_I \cdot Y_T \cdot Y_W \cdot YFL \tag{5.1}$$

$$SPLANT = SPRTND \cdot SPRTMAX \cdot Y_I \cdot Y_T \cdot \\ Y_W \cdot KSPRT \cdot YFL \tag{5.2}$$

where SEEDMX is the potential number of seedlings [plants/ha], SPRTND the potential of a species to produce sprouts [0,1], SPRTMAX the potential number of sprouts [stems/ha], KSPRT the test if any stump is capable of sprouting, i.e., SLMAX-SPRMIN where SLMAX and SPRMIN are the maximum and minimum diameters of a stump capable of sprouting [cm], and YFL a random number [0...1]. YI, YT, and YW are growth multipliers.

The initial growth of seedlings and sprouts are observed for 12 years as cohorts per tree species. The survival probability of seedlings (SURPRB) is assumed to increase as a function of seedling age with the following probabilities for different species (Kellomäki et al. 1987).

Species	Year since birth of a cohort											
	1	2	3	4	5	6	7	8	9	10	11	12
	Probability of survival											
Pinus sylvestris	0.1	0.2	0.6	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Picea abies	0.2	0.4	0.6	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Betula spp.	0.01	0.05	0.2	0.4	0.6	0.8	0.9	0.9	0.9	0.9	0.9	0.9

At the same time the survival capacity of seedlings (SURMUL) will increase as a function of the age of the seedling cohort

$$SURMUL = SURPRB + YFL \cdot (TOLER) \qquad (5.3)$$

where YLF is a random number [0...1] and TOLER [0...1] the sensitivity of seedlings to die.

Species	Year since birth of a cohort											
	1	2	3	4	5	6	7	8	9	10	11	12
	Sensitivity											
Pinus sylvestris	0.6	0.6	0.4	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Picea abies	0.6	0.4	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Betula spp.	0.6	0.6	0.6	0.5	0.4	0.2	0.1	0.1	0.1	0.1	0.1	0.1

The number of seedlings dying (NRODEAD, stems/ha) in a given year is

$$NRODEAD = IPDENS \cdot (1 - SURMUL) \qquad (5.4)$$

where IPDENS = NPLANT + SPLANT [stems/ ha]. If a seedling does not achieve a height of

Fig. 6. Outlines of calculation of number of seedlings recruited in the regeneration process.

1.3 m in 12 years (the expected age of a seedling reaching the height 1.3 m), the seedling will die (Valtakunnan metsien... 1986). The diameter growth at the stump level (10 cm above soil level) and the subsequent height of seedlings are calculated at the same time. The method for calculating the diameter growth is the same as that of established trees, but subjected to diameter growth at the stump height ($D_{0.1}$,cm). Seedlings reaching a height of 1.3 m during 12 years are treated as established trees.

In the *artificial* regeneration the initial stand is created in the planting by introducing trees with heights ≥ 0.1 m or optionally 1.3 m directly into the site, the initial stand being specified in regard to the density and diameter distribution (0.1 m or 1.3 m above soil level) per tree species. The height, mass, and other properties of seedlings and sprouts recruited into the stand in a given year are based on the diameter at stump height or breast height.

5.2 Growth

Trees. The growth of the *mass* of trees and their components is based on the diameter growth as in the original model, but the calculation of the diameter growth is thoroughly revised, putting more emphasis on the estimate of the growth and yield than in the original model. The diameter growth [cm a^{-1}] (0.1 m or 1.3 m above ground level) of a tree (Y) is a product of the potential diameter growth (Y_0, cm a^{-1}) and growth multipliers

$$Y = Y_O \cdot Y_I \cdot Y_T \cdot Y_W \cdot Y_N \cdot Y_C \qquad (5.5)$$

The potential diameter growth of trees is assumed to be the diameter growth not limited by temperature conditions and the availability of light, water, nitrogen and sub-zero temperature. In the boreal conditions, the availability of nitrogen appears to be the only factor enhancing the growth, if the supply of resources is increased (Axelsson 1984, Tamm 1991). The fertilizing experiments show that the diameter growth of stand-grown Scots pines could under an ample supply of nitrogen be even double with no growth disturbances compared to the unfertilized trees (Jonsson 1978). The same seems to be valid also for Norway spruce (Tamm 1961) and birch species (Viro 1975).

However, the growth response to nitrogen is differentiated in regard the growth before fertilization, i.e., the optimal growth is relative the current growth before fertilization and, thus to the diameter of trees (Malm et al. 1974, Gustavsen and Lipas 1975). Consequently, the potential diameter growth is calculated as a function of the growth of stand-grown trees (Y_E, cm a^{-1}), i.e., $Y_0 = 2 \cdot Y_E$, where $Y_E = G \cdot DBH \cdot \exp(DGRO \cdot DBH)$, DBH [cm] being the stem diameter at breast height, and G and DGRO parameters. The values of parameters G and DGRO were estimated based on the values of mean diameter growth obtained from the growth and yield tables for natural stands (Koivisto 1959) based on the standard statistical procedure (Table 2).

The *height* of trees is calculated optionally on the basis of Näslund's (1936) or Päivinen's (1987) height model. The *mass* of tree organs (foliage, branches, stem, roots) was calculated based on the allometric relations between the stem diameter and biomass of different organs, i.e. MASS(j) = paramA(j) $\cdot$ DBH$^{paramB(j)}$, where MASS(j) is the mass [kg] of component (foliage, branches, stem, roots) and paramA(j) and paramB(j) parameters specific for each tree spe-

Table 2. Parameters for growth of trees for southern Finland as specified for tree species for sites of *Myrtillus* type.

Parameter	Pine	Spruce	Pendula	Pubescent
G [a^{-1}]	0.3674	0.3311	0.8215	0.6000
DGRO [cm^{-1}]	−0.1261	−0.1192	−0.1782	−0.1990

cies. The mass of stem, branches, and roots are given including bark.

Ground vegetation. The model for the growth of ground cover is that developed by Kellomäki and Väisänen (1991). Each species of the initial community was labelled as pioneer, intermediate, or climax assuming that species occurring in the same manner in the successional process respond in the same way to light and nitrogen. The growth for each plant group (dG(t)/dt) was computed in the same manner as the tree growth, but the potential growth was limited by the availability of light and nitrogen

$$G_o(t) = \exp(BDGRO \cdot M(t)) \qquad (5.8)$$

$$\frac{dG(t)}{dt} = G_O(t) \cdot G_I(t) \cdot G_N(t) \qquad (5.9)$$

where G_o [gm^{-2}a^{-1}] is the potential growth, M [gm^{-2}] the actual mass of a particular species group, G_I and G_N the growth multipliers dependent on the availability of light and nitrogen, BDGRO a parameter, and t time in years.

The actual mass of a particular species group in any year is computed as the balance of the growth and death rates integrated over the preceding years. The death rate of each species group was assumed to be 5% of the standing crop (Mälkönen 1974). Dead material was converted to litter and, subsequently, to humus. Litter and humus were decomposed in the same way as litter and humus originating from the tree stratum.

5.3 Death

Death of trees induced by endogenic factors. The death of an established tree depends on the age of the tree and the environmental conditions acting through growth as in the original model, but the model is also revised to include the effects of fire, wind and insect attack on the risk of death. In *age-dependent* mortality a tree will die if the value of a uniform random number chosen for each tree is less than 2/AGEMAX, where AGEMAX is the maximum age of a tree species. This procedure results in a 0.5% probability of surviving to the maximum age of 400 years, the age-dependent mortality being stochastic. If the age of a tree is equal to the maximum age, the tree will die.

Age-independent mortality is determined by whether the diameter growth exceeds the mini-
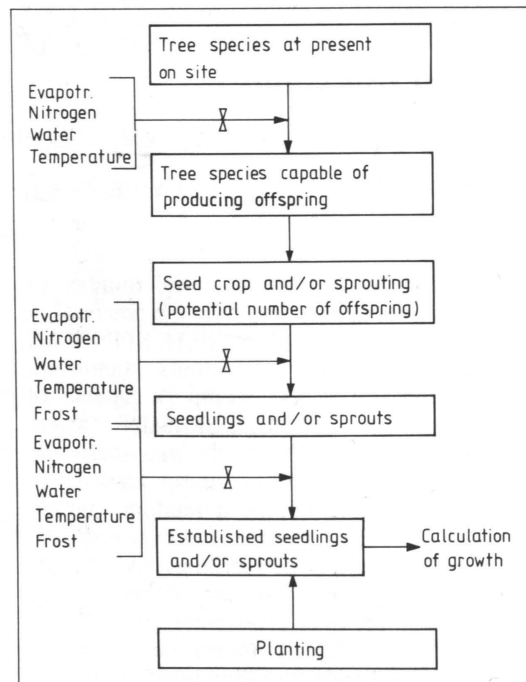
mum allowable growth. If diameter growth in the two previous years is < the minimum allowable growth, the tree is considered to have no growth. This implies that a tree would have a 1% chance of surviving 10 consecutive years of growth below the specified minimum growth. Two consecutive years of no growth will result in a 0.38 probability of a tree dying.

Death of tree organs. The death of tree organs (branches, foliage, roots) and dead trees form the litter. The mass of *woody* litter (stem wood, stem bark) is the sum of the woody mass of each dead tree, the mass being multiplied by 0.6 to approximate the change in wood density due to death. The mass of *foliage* litter [kg/ha] is obtained by multiplying the biomass of foliage by the inverse value of the retention time of foliage. If the diameter growth of a tree is, however, less than the minimum growth in the two previous years, the amount of litter is assumed to be one half that of a healthy tree. If a tree dies, all the foliage mass is treated as litter. The mass of *branch* litter [kg/ha] is assumed to be 0.003 · (Basal area) of the trees in the stand. The mass of *root* litter [kg/ha] is assumed to be 1.3 · (foliage litter) · (root/shoot-ratio).

Dead trees are eliminated from living trees and immediately converted to litter. Optionally, the dead trees will stand in order to simulate the occurrence of standing dead trees in the stand. In the latter case a dead tree will remain standing for a time period specific for each tree species. The retention time is 30 years for *Pinus sylvestris*, 20 years for *Picea abies* and 10 years for deciduous tree species.

Death induced by insects. Death due to insect attack is incorporated into the subroutine for death through a risk added to the age-dependent and age-independent mortalities, i.e., C = (k+r)/ AGEMAX, where C is the total risk of dying, k a parameter and r the risk of dying in insect attack, wild fire or windblow (Lauhanen et al. 1989). The risk of dying due to insect attack is simulated assuming that the insect attacks are inversely related to the growth efficiency (Larsson et al. 1983, Waring and Schlesinger 1985). The growth efficiency (E) is defined as the production of stem wood (G) per unit of needle biomass (N), i.e., E = G/N (g/g). The additional risk of a tree dying due to insect attack (r) is r = 1 – E. The consequent total risk of a tree dying is C = 2 · (1 + r)/AGEMAX, where C is the probability of the death of the tree and AGEMX the maximum age of the tree.

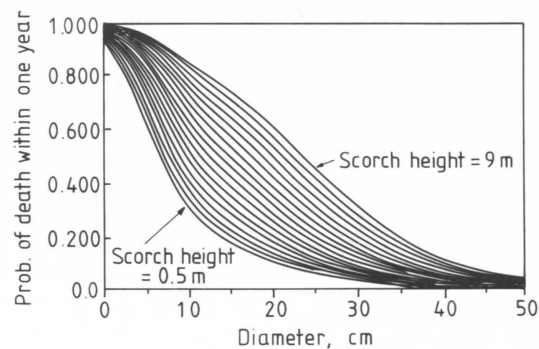*Death induced by forest fire.* In the case of fire-

Fig. 7. Risk of a tree dying due to wild fire as a function of the scorch height.

induced death the value of parameter r is based on the scorch height calculated in the subroutine for fire adapted from Kercher and Axelrod (1984b), but modified to account for the loss of nitrogen from the soil. The scorch height is a function of the fire intensity, wind speed, and air temperature. The fire intensity [W/m²] is a function of the wind speed [m/s], steepness of slope [%], moisture content of litter [%], mass of fuel [kg/m²] per fuel type, oven dry particle density of fuel [kg/m³] per fuel type, bulk loading of fuel type [kg/m³](fuel mass/fuel volume), mean surface area per unit volume of fuel type [cm⁻¹], heat content of fuel type [kJ/kg], mineral content fraction [0...1] of fuel type, and silica-free mineral content fraction of fuel.

Fuel on the site represents the litter of previous years, the living mass of seedlings and sprouts and the mass of ground vegetation. Fire occurs at given intervals. The probability of fire increases with the amount of time following the previous fire incident. The year of fire within the fire interval is random in such a way that the basic risk of fire (0 < p < 1) is compared to the random number [0...1]. If the value of the random number is greater than the basic risk, the year is a fire year. Thereafter the risk of dying is calculated as a function of the scorch height separately for trees with diameter > 12.7 cm and with diameters < 12.7 cm (Fig. 7).

The reduction of litter and humus due to fire is assumed to be 24% (Viro 1969). The organic material in soil is burnt in the order of needle and leaf litter, litter formed in ground cover, twig litter, dead trees DBH < 1 cm, dead trees 1 cm < DBH < 2 cm, etc. in classes of 1 cm or 2 cm up to 10 cm dead trees until the accumulation of burnt mass exceeds the total burnt mass,

i.e., 24% of the mass of forest floor and ground cover before the fire. At the same time the amount of nitrogen in the forest ecosystem will be reduced in the same proportion as nitrogen is bound in the fuel.

Death induced by wind was calculated with the help of a method developed by Lohmander and Helles (1987). The method calculates the risk of windblow, which is used in the subroutine for death to calculate the death of any tree affected by wind. The risk of tree death is related to the stand structure and management, i.e.,

$$rw = \frac{1}{1+e^z} \qquad (5.10)$$

where rw is the risk of windblow [0...1] and Z

$$Z = -7.22 - 4.19 \cdot 10^{-5} \cdot DBH^2 + 2.06 \cdot 10^{-4} \cdot \\ DHEIGHT^2 + 0.492 \cdot KV - ... -2.65 \cdot \\ SPECIES + 0.047 \cdot AGE + 16.9 \cdot \\ THINNING - ... -6.97 \cdot 10^{-7} \cdot POSITION \qquad (5.11)$$

where DHEIGHT is the height of dominant trees [m], KV the water relation in the site [0 = dry, 2 = moist, 3 = waterlogged], SPECIES the resistance of the species to windblow [Scots pine = 1, birch = 1, Norway spruce = 0], AGE the mean age of the dominant trees [a], THINNING a variable indicating the thinning pattern and POSITION the stand position in relation to other stands, which indicates the shelter from wind received by a particular stand from other stands. Furthermore,

$$(5.12)$$

$$THINNING = \frac{VTHINNING}{VBEFORE} \cdot (1 + TTHINNING)^{-1.686}$$

where THINNING [0...] is compiled from the volume of the stand before thinning (VBEFORE, m³ha⁻¹), the cutting removal in the thinning (VTHINNING, m³ha⁻¹), and the time in years since the latest thinning (TTHINNING, a).

6 Evaluation of the model

The evaluation of the present model is limited to the validation against measurements and sensitivity analysis of the model output to the values of selected parameters. The former indicates the precision and realism of the model, and latter pin-points the areas of major importance for the model behavior and future research needs (Swartzman and Kaluzny 1987). The evaluation of the model is limited to the growth and yield model omitting the effect of wild fire, wind, and insect attack on system behavior. The simulation experiments based on these subprocesses improve the understanding of system behavior rather than measure the precision of the model output.

The *output* of the model in terms of growth and yield was compared to the standard growth and yield tables (Koivisto 1959). The time course of stem volume in a Scots pine stand on a *Myrtillus* site given by the present model exceeded during the middle rotation (130 years) that expected on the basis of the growth and yield tables, but during the early and late rotation the model gave fairly similar values compared to the growth and yield tables. For Norway spruce the output of the model was fairly comparable to that in the growth and yield tables throughout

the rotation. In the case of birch the volume of pendula birch was much higher than that in the growth and yield tables throughout the rotation. For pubescens birch the model output during the early rotation was fairly similar to that in the growth and yield tables, but in the late rotation much lower. In the late rotation the combined volume of pendula and pubescens birch followed that in the growth and yield tables, which represent stands of unspecified combination of pendula and pubescens birches (Fig. 8).

The *sensitivity analysis* of the model was also limited to the parameters of the growth and yield models in the case of Scots pine. The values of the parameters were increased or decreased 10 % from the original values of the same parameters and the total model output in each case was compared to the output given by the original parameter value. This analysis indicated that the model output is most systematically (in all phases of the succession) sensitive to the parameters of the equations used to calculate the mass of different tree components based on stem diameter. In particular, the conversion of stem diameter to stem mass was important, as was converting the stem diameter to the crown projection area. In addition, the changes in the
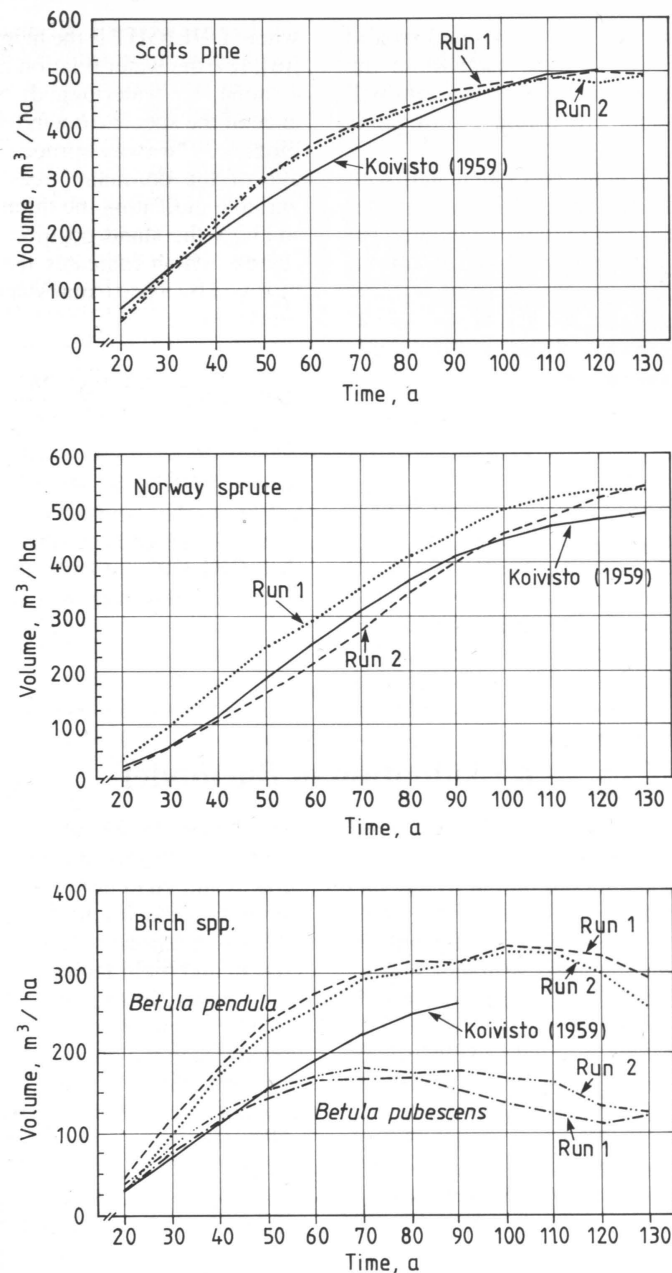
Fig. 8. Time course of stem volume in an unthinned Scots pine, Norway spruce and birch stands produced by the present model and the growth and yield tables on a site of *Myrtillus* type in southern Finland. It was assumed that the initial stand density was 4800 stems/ha with a diameter of 1.0 cm at breast height, the temperature sum 1300 d.d. and the annual precipitation 500 mm. Two separate calculations for each tree species are presented, each time series being a mean of ten replicates of the scenario.

parameters in calculating the light and nitrogen multipliers resulted in a substantial change in model output, but in these cases the reaction was not as systematic as in the case of tree allometry.

7 Computational example

An example of the model output is given in Fig. 9, which depicts the natural succession of a tree stand on a site of *Myrtillus* type in southern Finland. *Pinus sylvestris*, *Picea abies*, *Betula pendula*, and *Betula pubescens* were allowed to invade this sand loam site having a water holding capacity of 2.4 cm (in 30 cm of soil) at the wilting point, and 5.5 cm at the field capacity. The temperature and precipitation patterns for the Helsinki area were applied in the calculations (Table 3). At the beginning of the simulation the amount of litter and humus on the soil was 62 t ha^{-1}. Nitrogen deposition was 10 kg ha^{-1} a^{-1}. The total simulation time was 400 years. The output of the simulation is the mean of ten separate model runs.

The very early phase of the succession (stand age < 30 a) is characterized by a mixture of *Pinus sylvestris*, *Betula pendula*, *Betula pubescens*, and *Picea abies*. Thereafter *Pinus sylvestris* achieves dominance. However, *Picea abies* survives in the stand and its mass starts to increase about 150 years after the establishment of the initial stand. At the same time the mass of *Pinus sylvestris* starts to decrease due to the death of aging trees. *Betula* spp. survive in the stand more than 200 years. However, the mass of *Betula* spp. remains small since the light conditions below the stand do not support the regeneration and growth of *Betula* spp. The late succession is characterized by the gradual increase in the mass of *Picea abies*, which achieves dominance when 320 years have elapsed from the establishment of the initial stand. However, *Pinus sylvestris* survives to the end of the simulation in the form of tall trees, but *Pinus sylvestris* is not capable of regenerating due to the increasing shading by *Picea abies*.

The mass of *Pinus sylvestris* reaches its peak at the age of 100 years, the value of the mass being about 170 t ha^{-1}. At the same time the mass for *Picea abies* is about 30 t ha^{-1}, and for *Betula* spp. about 5 t ha^{-1}. The total mass of the stand is about 200 t ha^{-1}, equal to about 500 m^3 ha^{-1}. The total mass of the tree stand decreas-
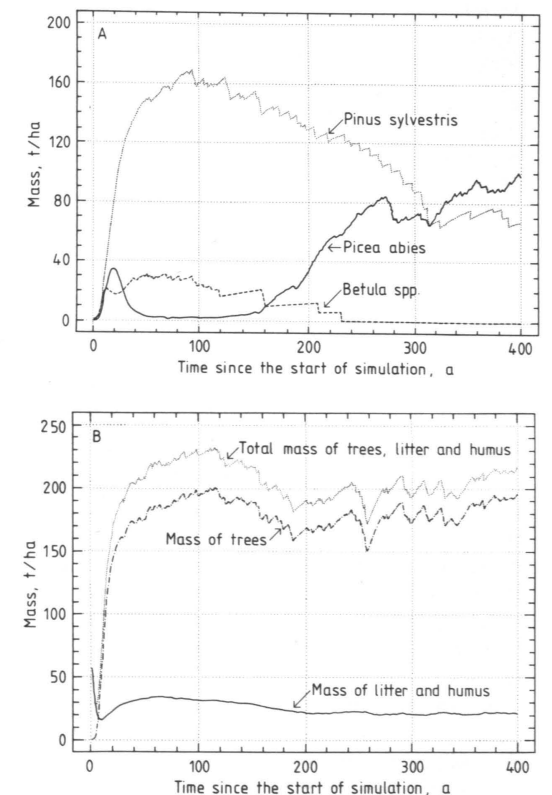

Fig. 9. Computational example of the succession of a tree stand as simulated with the aid of the present model. (A) Time course of above-soil mass of different tree species. (B) Time course of litter and humus on soil. Specifications of the simulation are given in the text and in Table 3.

es slightly after the peaking, but levels off at about 170–180 t ha^{-1} throughout the rest of the succession.

The time course of the mass of litter and humus is characterized by a drastic decrease at the very beginning of the succession. Thereafter the mass increases slowly in accordance with the growth of trees and the consequent litter

Table 3. Monthly temperature and precipitation patterns applied in calculations. The values represent the long-term (year 1960–1980) mean values for the Helsinki area.

Month	Temperature, °C		Precipitation, mm	
	Mean	SD	Mean	SD
January	–6.9	4.3	35	20
February	–7.3	4.5	27	14
March	–3.2	2.9	29	16
April	2.6	1.2	41	28
May	9.6	1.3	33	13
June	15.3	1.7	37	32
July	16.4	0.9	71	32
August	15.1	0.9	79	48
September	10.1	1.4	71	33
October	5.1	1.2	70	48
November	0.2	1.4	71	25
December	–4.1	3.0	54	28

fall. The mass of humus culminates later than the mass of the tree stand, the maximum value of the litter and humus on the soil being about 35–40 t ha^{-1}. During the late succession the mass of litter and humus is nearly constant following the slight decrease after culmination, indicating that the litter fall and the decomposition of litter and humus is balanced. The total accumulation of organic matter in the ecosystem during the late succession is about 190–210 t ha^{-1}, which is about 80–90% of that at the peak accumulation of mass in the forest ecosystem.

system will proceed. For example, for studies of the effects of changing climate on growth and yield the model seems to be a proper compromise between growth and yield tables and models based on the physiology of trees.

8 Conclusions

The present model can be characterized as a combination of growth and yield tables and a model for environmental conditions, i.e., the potential growth of trees is modified by the environmental conditions through factors limiting the growth. In other words, the mechanism of birth, growth, and death of trees is not modelled explicitly to the extent normally used in models of the physiology and ecology of trees. This limits the possibilities of understanding the processes of the ecosystem, but facilitates predictions of the development of the ecosystem with sufficient accuracy. In addition, the model is capable of adapting to changing conditions more easily than traditional growth and yield tables.

A detailed model for the ecology of a forest stand such as the present one effectively summarizes the results concerning the ecology of tree species and the nutrient cycle. In this respect the model outlines the utilization of the results of ecological studies and reveals the areas in which additional studies are needed to increase the reliability of the model computations. For example, it was quite evident that the response of different tree species to environmental conditions in terms of survival and growth is still poorly known. Therefore, more research is necessary to determine how different tree species respond to the availability of different resources in order to create a more solid basis for the proper silvicultural management of different tree species in changing conditions.

The present model is strongest in applications in which the growth and yield of different tree species and their mutual competition are related to the changing conditions determined at the regional level. Therefore, the model could serve as an option to anyone who is interested in growth and yield and how growth and yield are related to the availability of resources. In this respect the model is an extension of the traditional growth models (e.g. growth and yield tables) and also explicitly includes the effects of the environmental conditions. The model structure is still simple enough to facilitate long-term computations with an accuracy typical of the traditional growth models. At the same time the model allows the user to study the effect of silvicultural management on the forest ecosystem.

The applications of the model in growth and yield studies are limited within the rotations normally applied in Finland since the material used for the estimation of the basic functions of the growth model represents this range. Computations outside this range will yield results with greater uncertainty, but still properly demonstrate how the development of the forest eco-

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