A simulation model for the succession of the boreal forest ecosystem

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TIIVISTELMÄ: POHJOISEN HAVUMETSÄN SUKKESSIOTA KUVAAVA SIMULOINTIMALLI


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.


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, Kausela 1990).

The successional processes in boreal conditions create a forest structure characterized by gap-phase dynamics, i.e., succession is only restarted 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-Bayouni et al. 1984, Kercher and Axelrod 1984a, b) in modelling the dynamics of a tree stand since Botkin et al. (1972) introduced the Jabowka model for describing the competitive process in multi-species community.

2 Model structure

2.1 Dynamics of tree stand

The dynamics of the forest ecosystem is assumed 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 processes 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 of a stand (NM, i = species) of individuals of each species can be written using the principle that the net growth of any tree in the year t equals the gross growth of that tree component minus the senescence of the same component. Thus,

\[ N(t) = N(t-1) + GN(t) - DN(t) \]  

(2.2)

where \( N(t) \) is the number of trees, \( N(t-1) \) is the number of trees in the previous year, \( GN(t) \) is the growth of trees, and \( DN(t) \) is the death of trees.

The dynamics 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,

\[ B(t) = BR(t) + GBR(t) - DBR(t) \]  

(2.3)

where \( B(t) \) is the biomass of a tree, \( BR(t) \) is the biomass of growth, \( GBR(t) \) is the growth biomass, and \( DBR(t) \) is the death biomass.

The effect of wild fire and windblow is introduced through the subroutines for kill, which affects the risk of a tree dying at a given moment. The site conditions and the type of 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 occurrence 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 ecosystem. 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).

2.2 Dynamics of environment

The light conditions in a stand are controlled by the dynamics of gaps, which is determined by the number and properties of trees in a stand. Temperature 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).

\[ ASW(k) = ASW(k-1) + PRECIP(k) - EVAP(k) - RUNOFF(k) \]  

(2.6)

The dynamics of available nitrogen (AVAILN) is determined by the nitrogen released (TMIN) in decomposition of organic matter in soil, desorbed from the atmosphere (NDEPOS), immobilized (TNMGB) in the decomposition of organic matter in soil and wash-away (NWASH) from the site, i.e.,

\[ AVAILN(t) = AVAILN(t-1) + TMIN(t) + NDEPOS(t) - NIMOB(t) - NWASH(t) \]  

(2.7)

where \( n \) indicates the nitrogen concentration of organic matter (%), dec the decomposition rate (%) and imm the immobilization rate (%). The rate of decomposition and immobilization are assumed to be related to the quality of organic matter (C, nitrogen, carbon).

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 decompositions. These subroutines are linked by the multipliers to the demographic subroutines (birth, growth, kill), which compute the population dynamics. 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 type of 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 occurrence 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 ecosystem. 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.

\[ RT(k) = T(k) + VTK(k) \cdot Z(k) \]  

(3.1)
Fig. 1. Outlines of the model.

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

$$\text{DEGR} = \sum_{k} \text{max}[0, RT(k)-5^\circ C] \cdot \text{DAYS}(k)$$  \hspace{1cm} (3.2)$$

where $5^\circ C$ 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 ontogenetic 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

$$\text{MEAN}(i) = RT(i) + VT(i) \cdot Z(i)$$  \hspace{1cm} (3.3)$$

$$\text{TMIN}(i) = A \cdot RT(i) + B$$  \hspace{1cm} (3.4)$$

where MEAN(i) is the mean temperature and TMIN(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 water 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.

Fig. 2. Outlines of the calculation of decomposition of litter and humus and mineralization of nitrogen.
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. \( G = G_1 \cdot M_1 \cdot M_2 \), where \( G \) is growth and/or regeneration, \( G_1 \) growth and/or regeneration in optimal conditions and \( M_1, M_2 \) 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 (Survase 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 \( \text{TS}_{\text{lign}} \) (day °C, threshold temperature +5 °C). The end of lignification is attained whenever \( \text{TS}_{\text{lign}} \) exceeds the critical value \( \text{TS}_{\text{crit}} \).

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 \( M_{\text{chill}} \) is

\[
0, \quad \text{if } T(i) \leq -3.4°C \quad (4.1)
\]

\[
M_{\text{chill}} = a_i \cdot T(i) + a_2, \quad \text{if } -3.4°C < T(i) \leq 3.5°C
\]

\[
M_{\text{chill}} = a_i \cdot T(i) + a_3, \quad \text{if } 3.5°C < T(i) \leq 10.4°C
\]

\[
0, \quad \text{if } T(i) > 10.4°C
\]

where \( T(i) \) is the prevailing air temperature, \( a_i = 0.159 \text{ CU day}^{-1} \text{ °C}^{-1}, a_2 = 0.506 \text{ CU day}^{-1}, a_3 = -0.159 \text{ CU day}^{-1} °C^{-1}, \) and \( a_3 = 1.621 \text{ CU day}^{-1} \).

State of chilling at a given day \( t \), \( \text{S}_{\text{chill}}(i) \), is calculated by integrating rate of chilling, \( M_{\text{chill}} \), from the end of lignification to the day \( i \). Rest completion takes place if \( \text{S}_{\text{chill}} \) exceeds the critical value \( \text{CU}_{\text{crit}} \).

During the quiescent phases 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 \( M_{\text{forcing}} \) is

\[
M_{\text{forcing}} = \frac{a_4}{1 + e^{-(T(i) - T_0)/a_5}}, \quad \text{if } T(i) \leq 0°C \quad (4.2)
\]

\[
M_{\text{forcing}} = 0, \quad \text{if } T(i) > 0°C
\]

where \( T(i) \) is the prevailing air temperature, \( a_4 = 28.4 \text{ FU day}^{-1}, a_5 = 0.185 \text{ °C}^{-1}, \) and \( a_6 = 18.4°C \).

State of forcing at a given day \( t \), \( \text{S}_{\text{forcing}}(i) \), is calculated by integrating rate of forcing \( M_{\text{forcing}} \) from rest completion up to the day \( i \) with bud burst takes place, when \( \text{S}_{\text{forcing}} \) attains a critical value \( \text{FU}_{\text{crit}} \) (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 is

\[
JF(i) = \frac{\text{NL}(i) + a_i \cdot \text{TS}_{\text{lign}}(i)}{a_i}, \quad (4.3)
\]

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

Annual course of frost hardiness. It is assumed that a stationary frost hardiness, \( H_{\text{sta}} \) attained in any constant temperature, that the value of \( H_{\text{sta}} \) depends linearly on prevailing temperature, and that the rate of change in actual hardness \( H \) increases with the growing difference between the actual hardness and stationary hardness \( H_{\text{sta}} \) (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 hardness.

The annual cycle is divided into three periods of frost hardness, and the calculation of \( H_{\text{sta}} \) 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 hardness and no potential for frost hardening, i.e., stationary frost hardness is a constant ($H_i$).

$$H_{w,i} = H_i$$

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

$$H_{w,i} = H_i - \frac{H_i - H_{i-1}}{NL_i - NL_{i-1}} (NL_i - NL_i) + H_i$$

where $NL_i$ is the prevailing light length, $NL_i$ and $NL_{i-1}$ are threshold values of night length, and $H_i$ and $H_{i-1}$ are values of stationary frost hardness in night lengths below $NL_i$ and above $NL_{i-1}$, respectively.

During the hardening period, frost hardness fluctuates according to air temperature (Repo et al. 1990). During this period, $H_{w,i}$ is

$$H_{w,i} = H_i - \frac{H_i - H_{i-1}}{T_i - T_{i-1}} (T_i - T_i) + H_i$$

where $T_i$ is the prevailing air temperature, $T_i$ and $T_{i-1}$ are threshold values of air temperature,

$$T_{i-1} = \text{const}$$

and $H_i$ and $H_{i-1}$ are values of stationary frost hardness obtained in temperatures above $T_i$ and below $T_{i-1}$, respectively (Fig. 4).

Rate of change in frost hardness, $dH_i/dt$, is calculated during each of the three periods as follows

$$dH_i/dt = \tau^{-1} ((H_n(i) - H(i))$$

where $\tau$ is the time constant for attaining the stationary frost hardness, $H_n(i)$ the stationary frost hardness, and $H(i)$ the actual frost hardness. Actual frost hardness is determined by integrating Eq. (4.7) up to the moment $i$.

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

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

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 $Y$, over the year

$$Y = \frac{1}{365} \sum_{i} GF(i)$$

The multiplier $Y$ is used in the succession model at the annual level, low values of $Y$ 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 hardness 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 hardness, $H$. The three curves illustrate cases where $H = -6^\circ C$, $H = -10^\circ C$, and $H = -20^\circ C$, respectively.

5 Calculation of dynamics of tree stand

5.1 Regeneration

The subroutines for birth allow the regeneration of a tree stand naturally through seedling 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 are 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 offsprings due to seeding and sprouting. The potential number of offsprings (TPLANT = NPLANT + SPLANT) is reduced by the growth multipliers

$$NPLANT = \text{SEEDMX} \cdot Y_i \cdot Y_{w} \cdot Y_{f}$$

$$SPLANT = \text{SPRTND} \cdot \text{SPRTMAX} \cdot Y_i \cdot Y_{f}$$

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...1], YL, 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 (SURPR) is assumed to increase as a function of seeding age with the following probabilities for different species (Kellomäki et al. 1987).
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, Tammi 1991). The fertilizing experiments show that the diameter growth of stand-grown Scots pines could under an ample supply of nitrogen be even double without growth disturbances compared to the unfertilized trees (Jonsson 1978). The same seems to be valid also for Norwegian spruce (Tammi 1961) and birch species (Viro 1975).

However, the growth response to nitrogen is differentiated in regard to 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 ($Y_{E_i}$, cm a$^{-1}$), i.e., $Y_E = Y_{E_0} + Y_{E_1} \cdot G_{DGRO}$, where $Y_{E_0}$ is 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 (Kroivisto 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., $M(i)=\frac{g(i)}{p(i)} \cdot B(i)$, where $M(i)$ is the mass [kg] of component (foliage, branches, stem, roots) and $p(i)$ and $B(i)$ parameters specific for each tree species.

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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Pine</th>
<th>Spruce</th>
<th>Pandoela</th>
<th>Pubescens</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G$ [a$^{-1}$]</td>
<td>0.3674</td>
<td>0.3311</td>
<td>0.8215</td>
<td>0.6000</td>
</tr>
<tr>
<td>DGRO [cm$^{-1}$]</td>
<td>-0.1261</td>
<td>-0.1192</td>
<td>-0.1782</td>
<td>-0.1990</td>
</tr>
</tbody>
</table>

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 ($Y_E$) is a product of the potential diameter growth ($Y_{E_0}$, cm a$^{-1}$) and growth multipliers.
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 \cdot (Basal area) of the trees in the stand. The mass of root litter [kg/ha] is assumed to be 1.3 \cdot (foliage litter) \cdot (root/shoot-ratio).

Dead trees 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 treated as the subroute for death through a risk added to the age-dependent and age-independent mortalities, i.e., \( C = (k+r) \cdot AGEMAX \), where \( C \) is the total risk of dying, \( k \) a parameter of dying in insect attack, \( r \) a risk of dying to the random number \( 0...1 \). 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 windthrow, which is used in the subroute 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.,

\[
\text{rw} = \frac{1}{1 + e^{(5.10)}},
\]

where \( \text{rw} \) is the risk of windthrow \([0...1]\) and \( Z = -7.22 \cdot 4.19 \cdot 10^{-4} \cdot DBH + 2.06 \cdot 10^{-4} \cdot \text{DHEIGHT} + 0.492 \cdot \text{KVA} - 2.65 \cdot \text{SPECIES} + 0.047 \cdot \text{AGE} + 16.9 \cdot \text{THINNING} - 6.97 \cdot 10^{-1} \cdot \text{POSITION} \)

**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** is in terms of growth and yield was compared to the standard growth and yield tables (Koivist 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 systemically (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

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

\[
\text{DHEIGHT} = \text{AGE} + \text{VTHINNING} \cdot (1 + \text{VBEFORE}) \cdot 1.086
\]

where **VTHINNING** = 0.031 is compiled from the volume of the stand before thinning (**VBEFORE**, m³/ha), the cutting removal in the thinning (**VTHINNING**, m³/ha), and the time in years since the latest thinning (**TTHINNING**, a).
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 m³ ha⁻¹. The total mass of the tree stand decreases 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.

<table>
<thead>
<tr>
<th>Month</th>
<th>Temperature, °C</th>
<th>Precipitation, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>January</td>
<td>-6.9</td>
<td>4.3</td>
</tr>
<tr>
<td>February</td>
<td>-7.3</td>
<td>4.5</td>
</tr>
<tr>
<td>March</td>
<td>-3.2</td>
<td>2.9</td>
</tr>
<tr>
<td>April</td>
<td>2.6</td>
<td>1.2</td>
</tr>
<tr>
<td>May</td>
<td>9.6</td>
<td>1.3</td>
</tr>
<tr>
<td>June</td>
<td>15.3</td>
<td>1.7</td>
</tr>
<tr>
<td>July</td>
<td>16.4</td>
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</tr>
<tr>
<td>August</td>
<td>15.1</td>
<td>0.9</td>
</tr>
<tr>
<td>September</td>
<td>10.1</td>
<td>1.4</td>
</tr>
<tr>
<td>October</td>
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<td>1.2</td>
</tr>
<tr>
<td>November</td>
<td>0.2</td>
<td>1.4</td>
</tr>
<tr>
<td>December</td>
<td>-4.1</td>
<td>3.0</td>
</tr>
</tbody>
</table>

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. This in turn respects the model the utilization of the results of ecological studies and reveals the area in which additional studies are needed to increase the reliability of the model calculations. 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 this 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 ecosystem 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.

References


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Silva Fennica 26(1)

Growth response of young Scots pines to artificial shoot breaking simulating moose damage

Risto Heikilä & Kari Löytyniemi

TIIVISTELMA: HIRVIJOITUSTA JÄLJITTELEVÄN VERSON KATKAISUN VAikutus Nuoren Männyn Kehtiykseen


The main stem of young pine (Pinus sylvestris) trees was cut off halfway along the current leading shoot and the two previous years’ leading shoots. Trees of the same size were chosen as controls before treatments. The experiment was inspected ten years after artificial stem breakage. Removing the current leading shoot and the second shoot did not essentially affect the height and diameter growth of the trees. Removal down to the third shoot reduced the height as well as diameter growth. The average loss in growth was equivalent to less than one year’s growth. When the stem was cut off at the second or third shoot, stem crookedness and the presence of knots resulted in stem defects that will subsequently reduce the sawtimber quality. A high proportion of the stem defects will obviously still be visible at the first thinning cutting. Removing injured trees as pulpwod and pruning the remaining parts of cut stems evidently improves the quality of pine stand with moose damage.


Keywords: Pinus sylvestris, stems, breakage, Alces alces, damage, growth, timbers, quality.

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