Shoot-based three-dimensional model of young Scots pine growth

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Abstract

The aim of the research was to create an algorithm simulating height-diameter relations in a pine tree subjected to various environmental impacts. The model is based on explicit description of light competition of the Scots pine twigs in three-dimensional space. The model is empirical and results from the measurements of correlations between shoots and buds in Scots pine that were made in the field. The development of the root system is not considered by the model.

In simulation experiments it was demonstrated that: (i) the stand-grown pines have a higher height/diameter ratio than an open-grown model tree; (ii) an extremely high height/diameter ratio leads the tree to death; (iii) a tree suppressed for a sufficiently long time does not respond to better conditions; (iv) the diameter growth is much more sensitive to environmental change than the height growth. The model trees had the same growth parameters in every simulation. The simulated growth reactions are accounted for by self-adjustments of the model structure to the imposed conditions.

Keywords: Growth, plant; Light; Morphology; Pine

1. Introduction

There is a growing understanding in plant population biology that many effects of population life originate from interactions between individuals and should be explained on that basis (Clark, 1990).

The way in which trees influence each other is clear at a qualitative level and has not been sufficiently studied in quantitative terms. It has been noticed long ago that trees grown in an open space have relatively more decurrent crowns, lower heights, and thicker trunks than forest trees. It would then be desirable to be able to predict what the sizes of trees would be at a certain age provided a definite initial spacing or other conditions are known. This is not an easy task because a true validation of the prediction should be based on experimental recordings of forest stand growth. Regrettably, the lifespan in trees is too long to permit direct experimenting with their growth.

For this reason we started developing simula-
tion algorithms to study mutual influences of trees in stands. It was understood that studying interactions between trees cannot proceed without taking account of internal structures of trees. Our previous paper (Gavrikov and Sekretenko, 1992) dealt with three-dimensional growth of Scots pine (*Pinus sylvestris* L.) crown modeled as a population of twigs. The twigs influenced each other via screening light coming from above. The idea that a population of plants can be studied at the level of independent plant parts has been developed by Harper and White (1974).

Studies of branching habit and the shoot growth of various conifers have been reported before (Little, 1970; Treskin, 1973; Cochrane and Ford, 1978; Wilson, 1989a, b; Kurttio and Kellomäki, 1990; Gavrikov and Karlin, 1993; Kurth, 1994). Kellomäki and Kurttio (1991) made a very detailed model of Scots pine modular growth. The present study gives a simplified description of Scots pine branching habit. But at the same time, our model takes into consideration competition among shoots. The amount of foliage on the tree is strongly correlated to the cross-sectional area of the stem at the base of the live crown (Shinozaki et al., 1964). It has been reported in a number of studies (Hari et al., 1985; Kaibiyainen and Hari, 1985; Kaibiyainen et al., 1986) that stem–foliage correlations in Scots pine are very strong. Therefore, for this proportionality to take place, there has to be a continual adjustment between stem and crown growth.

Table 1
List of relationships used to simulate light-dependent growth of population of twigs

<table>
<thead>
<tr>
<th>No.</th>
<th>Determined parameter (y)</th>
<th>Independent variables (x)</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sum of bud sizes in whorl</td>
<td>Diameter of twig</td>
<td>( y = 4.37 \cdot x - 6.22 )</td>
</tr>
<tr>
<td>2</td>
<td>Number of buds in whorl</td>
<td>Diameter of twig</td>
<td>( y = \text{round}(1.1 \cdot x - 0.72), y \leq 9 )</td>
</tr>
<tr>
<td>3</td>
<td>Diameter of a bud in whorl</td>
<td>Number of buds in whorl, relative size of the bud (largest, second largest)</td>
<td>( y = \begin{cases} 9, &amp; y &gt; 9 \ \text{matrix of coefficients in Table 3} &amp; \end{cases} )</td>
</tr>
<tr>
<td>4</td>
<td>Length of bud</td>
<td>Diameter of bud</td>
<td>( y = 2.4455 \cdot x - 0.9377 )</td>
</tr>
<tr>
<td>5</td>
<td>Max length of daughter twig</td>
<td>Length of parent bud</td>
<td>( y = 30.3 \cdot x - 81.22 )</td>
</tr>
<tr>
<td>6</td>
<td>Max diameter of daughter twig</td>
<td>Diameter of parent bud</td>
<td>( y = 0.59 \cdot x^{1.5948} )</td>
</tr>
<tr>
<td>7</td>
<td>“Illumination” of twig</td>
<td>Shadows ((x)) of (N) twigs above, size of the “sky” ((X))</td>
<td>( y = X - \sum_{i} x_i )</td>
</tr>
<tr>
<td>8</td>
<td>Relative index of light-dependent growth</td>
<td>“Illumination” of twig</td>
<td>( y = \begin{cases} 2 \cdot x, &amp; x \leq 0.5 \ 1, &amp; x &gt; 0.5 \end{cases} )</td>
</tr>
<tr>
<td>9</td>
<td>Actual sizes of daughter twigs</td>
<td>Max sizes of daughter twigs ((x_1)), index of light-dependent growth ((x_2))</td>
<td>( y = x_1 \cdot x_2 )</td>
</tr>
</tbody>
</table>
Fig. 1. A flow diagram of the light interception and twigs growth simulation. The block "Crown-stem imbalance" refers to the modelling of relations between the growth of the twig population and the diameter growth of the stem. The part of the model is clarified further in text.

2. The model

2.1. Simulation of light-dependent growth of crown

Three-dimensional growth of Scots pine crown treated as a population of twigs has been considered in a paper by Gavrikov and Sekretenko (1992). In this subsection, we briefly outline the main approach to simulating light-dependent growth of shoots. This is necessary for understanding the whole structure of the model because the crown simulation is one of the two main parts of the model.

The algorithm of the simulation of light-de-
Pendent growth of twigs is presented in Fig. 1. Rules which control shoot reproduction, growth, and mortality were developed on the basis of field studies of shoot–bud correlations in Scots pine. These rules are summarized in Table 1. The statistics for the relations are given in Table 2.

The coefficients given in Table 3 serve to calculate diameters of buds in a particular whorl. The coefficients are based on the measurements of real winter bud whorls (Gavrikov and Sekretenko, 1992). Suppose, there is a whorl of five buds; every bud may be ascribed with an index of relative size: 1, the largest; 2, second largest, etc.; the sum of bud diameters presents a certain value. In order to estimate, for example, the largest bud diameter, one should multiply the sum by 0.27 (Table 3, number of buds = 5, the relative size of the bud = 1).

Shadows of twigs which darken a subject twig were calculated according to the data published by Smolander et al. (1987), where the authors photographically measured projections of Scots pine shoots. A linear dependence between the photographically measured projection and the total surface of needles attached to the shoot was reported. The coefficient of the relationship is equal to 0.55, which means that the projection is 0.55 of the total surface of needles.

An important point developed in the previous paper (Gavrikov and Sekretenko, 1992) was an approach of maximal sizes of twigs. The maximal size (length, diameter) of a twig is the size that the extending bud achieves under best conditions of growth.

The maximal size of a twig can be estimated experimentally. In our work we used a heavy debudding treatment to estimate maximal lengths and diameters of twigs in growing young trees of Scots pine. All winter buds but one in every upper branch of the pines were excised. The remaining bud was considered to achieve its maximal size as no bud-competitors interfered with its development. It was found that the maximal length of the twig depends linearly on the bud length (Table 1, no. 5), with the maximal twig diameter depending on the bud diameter in a slightly non-linear way (Table 1, no. 6).

### 2.2. Algorithm of interaction between crown and stem

#### 2.2.1. Growth control

There are two main factors that determine actual sizes of twigs expanding from a bud of a given length and diameter. The first is the relative illumination of the subject parent twig. Some studies (Beadle et al., 1985) assert that the photosynthesis of single shoots of Scots pine is primarily dependent on the light intensity. This seems to be true for the majority of shoots situated in the

<table>
<thead>
<tr>
<th>Number of buds in whorl</th>
<th>The relative diameter of a bud among other buds in the same whorl</th>
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<tr>
<td></td>
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<td>9</td>
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</table>

*Every line corresponds to a bud whorl. The sum of all numbers in every line is equal to 1, which means that the sum of diameters of all buds in a whorl is assumed to correspond to 100%. The buds in every whorl are not equal in size. There is always the largest bud (the relative size = 1) and the smallest one corresponding to the last number in the subject line (the relative sizes are 2 through 9). In order to receive the diameters of all buds in a whorl, one should multiply the sum of diameters of all buds by the coefficients from that line that corresponds to the number of buds in the whorl.*
depth of the crown layer. However, the upper shoots never suffer from lack of light, and if they slow the growth, this implies their dependence on other than light factors.

In this paper we take into consideration the proportionality between foliar mass and the sapwood cross-sectional area. There are many studies reporting strong relationships between some measure of the total foliage amount (surface, mass) and dbh, or circumference, or area of sapwood of the stem (Barclay et al., 1986; Jokela et al., 1986; Magnussen et al., 1986; Hungerford, 1987). This may mean that the crown contains as much foliage as is allowed by the stem size.

In particular, Kaibiyainen et al. (1986) found that the needle mass in Scots pine (MN, g) is related to the area of sapwood (SS, cm²) at 1.3 m by as follows

\[ MN = 39.8 \cdot SS, \quad R^2 = 0.88. \]  

Eq. 1 was used in the present model to estimate the amount of needles in the crown of Scots pine by the actual area of sapwood in a lower part of the stem.

The foliage amount has a much higher potential of increase than the stem because the shoots act as a population-like system. At a moment, the foliage amount may exceed the figure predetermined by the cross-sectional area of the stem. The imbalance between foliar mass and the sapwood cross-sectional area (IB) may be expressed as follows

\[ IB = \frac{MN}{W} \]  

where \( W \) stands for the actual mass of needles. The way to obtain an estimation of \( W \) will be specified in the next subsection.

The imbalance between the cross-sectional area and the needle mass was considered to be one of the two factors of the growth control. A twig in the model grows according to the following rules

\[ AS = \min\{IB, LDG\} \cdot MS; \quad LDG, IB \leq 1 \]  

where \( AS \) is the actual size of a twig, \( MS \) is the maximal size of the twig, \( LDG \) is the index of relative light-dependent growth of the twig. The quantities \( AS \) and \( MS \) have dimensions of a linear measure. Eq. 3 is obviously the Liebig principle of limiting factors.

To summarize, either the index of light-dependent growth or the foliage-stem imbalance controls the twig growth in the model. To decide which factor is the limiting one, the algorithm calculates the IB value estimating, on the one hand, the total needle biomass and, on the other, the area of the sapwood. The following subsections will deal with these parameters.

2.2.2. Estimation of needle mass from twigs

Actually no needles are considered in the model. That is why in order to estimate the total amount of foliage in the crown a recalculation is used at every step of computing.

The mass of needles attached to a twig is connected to the twig size. The estimation of the mass in the model was done by means of the following relationship (Tzel’niker, pers. commun.)

\[ TW = 0.27 \cdot L, \]  

where \( TW \) stands for the ovendry mass of needles (g), \( L \) is the length of the twig (cm).

Further, one can note that twigs in the model correspond to 2-year-old shoots of Scots pine observed in summertime. Therefore, the shoots bear 2-year-old needles. Studies on the above-ground biomass of pine stands in Siberia (Stakanov, pers. commun.) show that there is a fairly constant proportion of 2-year-old needle mass in the total mass of the canopy needles.

For example, the percentage of the 2-year-old needles in a young thinned pine stand is 27.8%, while the value amounts to 30% in an intact stand. These figures are very close to each other in spite of the fact that the total needle biomass in the thinned stand is twice as high (Stakanov, pers. commun.). Thus, the coefficient 0.29 reflects approximately the proportion of 2-year-old needle mass in the total amount of needles in the tree crown.

The procedure for estimating the total needle biomass (\( W' \)) is as follows. The use of the coefficient value is only justified if the tree is older than 5 years, 5 years being the maximal longevity of needles (Stakanov, pers. commun.). For this reason, the coefficient 0.29 was applied starting from the time when the model tree was 5 years
old. In the interval 1–5 years the coefficient was estimated by a linear declining function such that the proportion of the 2-year-old needles at the first step was 1.0 and at step 5 it equaled 0.29. Therefore, the total amount of needles in crown was estimated by summing up needles of all 2-year-old twigs and dividing the sum by 0.29. The result of the procedure corresponds to the quantity $W$.

2.2.3. Problem of tree ring growth prediction

A prediction of sapwood cross-sectional area requires first of all the understanding of what determines tree ring width. The process involves many subtle mechanisms that are not quite clear, at least quantitatively. While climate-dependent growth of a tree ring has been a subject of thorough research (Fritts et al., 1991) the accretion of the stem controlled by crown factors has not been sufficiently investigated yet.

It is clear that the cambial-cell division in every part of the stem consumes assimilates from the crown. On the other hand, quantitative relationships that connect the crown size to the cambium growth are not known. Therefore, the predictor of ring width developed here is hypothetical and based primarily on logical considerations.

The stem of the tree is modeled here by a horizontal section from the lowest part of the trunk (Fig. 2). We consider how a particular twig influences the growth of the horizontal section. The basic hypothesis is that the bigger a twig, the greater is its influence on the growth of the cross-section of stem. It is also natural to hypothesize that the more distant a twig from the stem section, the smaller is its effect on the stem growth.

It is known that the path of assimilates from a Scots pine branch down the stem is a narrow path (Hansen and Beck, 1990). This allows one to avoid a complicated surface geometry of trees. Suppose therefore that the stem section growth depends on all individual twigs in the following simple manner:

$$S_j = \sum_{i=1}^{N_j} \left( \frac{L_i}{WB_i} \right)_j$$

where $L$ is the length of the twig, $WB$ is the distance between the twig and the stem section along all branches, $i$ is the number of the twig, $N$ is the total number of twigs in the year $j$. The dimensionless quantity $S$ describes the general relationships between the crown and the cross-section. The more twigs there are, the bigger they are, and the less distant they are from the cross-section, the bigger is the value $S$. And the faster is the cross-section expected to grow.

The value $S$ has, further, to be converted into the real width or area of the model tree ring. It is here that we are facing the problem of stem growth prediction in the model. For example, the value of $S$ may be very high at some step of growth. The model must not allow tree ring to be anomalously big in this case. So, we need an upper limitation of the growth.

Real biological tissues always have upper limits of the growth rate, because cells can not divide too quickly. This is relevant to the cambium growth as well. There has to be the maximal number of cells produced annually by a cell of cambium.

The estimation of maximal ring growth was done in two ways. The first way consists in considering the maximal observed number of xylem cells produced by a cell of cambium. Observations (Stasova, pers. commun.) show that a cell of Scots pine cambium can produce annually not more than 150–200 cells of the xylem. The average area of a xylem cell horizontal section in Scots pine is 0.0016 mm², with the tangential length of the cambium cell being approximately...
0.04 mm. This means that 1 mm of the cambium circumference can produce from 6 up to 8 mm² of new xylem.

Another estimation was made by a direct measuring of the length of circumference of the former cambium (fall wood) and the area of the ring produced by the cambium. A number of young, actively growing trees were found in the field and the upper 3-year-old parts of the stems were taken for the measurements. The maximal observed ratio between the area of the last ring and the circumference of the former cambium was 8.05 mm²/mm, which corresponds to the independent estimation made above. The values of $S$ per 1 mm of the former cambium for the 3-year-old tops of the trees ranged from 0.0468 up to 0.0982.

Finally, it was assumed in the simulation experiments that the maximal growth of stem circumference was 6 mm² of new ring per 1 mm of circumference. The maximal growth in the simulations takes place at the relative value of $S = 0.08$. Therefore,

$$ANX = \begin{cases} 6 \cdot \text{CIR}, & S/\text{CIR} > 0.08 \\ 6 \cdot S/0.08, & S/\text{CIR} < 0.08 \end{cases}$$  \tag{6}$$

where $ANX$ is the area of new xylem (mm²), CIR is circumference of the stem section.

### 2.2.4. Active section of stem

Generally, the stem section contains sapwood and heartwood. It is not possible yet to determine a quantitative relationship that allows one to pre-

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**Fig. 3.** A flow diagram of the model for one cycle of computing (i.e., for one "year"). Variables: $i$ denotes the set of twigs, $J$ is year of computing, $N$ is number of twigs, $L$ is length of twig, $WB$ is distance between a twig and the stem cross section along the axes of growth, $WH$ defines to which whorl belongs a twig, $W$ is total mass of needles on the twig, CIR is circumference of the stem cross-section for the year $J-1$, $MX$ is maximal square of new xylem that can be produced by 1 mm of circumference, $ANX$ is actual area of new xylem, SS is active section of stem, IB is variable of crown-stem imbalance for the year $J+1$. 

- Simulation of light-dependent growth of twigs, Fig. 1
- Parameters of twigs $N, L_i, WB_i, WH_i$
- Number of whorls with twigs, NW
- Total mass of needles $W = \sum_{i=1}^{N} 0.27 L_i$
- Parameter of influence of crown on stem growth $N, L_i, WB_i$
- Initial circumference of stem, CIR
- Max square of new ring, $MS = \text{CIR} \cdot MX$
- Active section of stem $SS = \sum_{j=1}^{J} ANX_j$
- Estimation of crown-stem imbalance $IB = \frac{SS \cdot 39.8}{W}$
dict the rate of transformation of sapwood rings into the heartwood rings.

On the other hand, Kaibiyainen and Hari (1985) experimentally demonstrated that the number of the last rings that conduct water (i.e., belong to sapwood) approximately corresponds to the number of living whorls. Therefore, the estimation of the active section of stem can be based on a simple rule: the inner border of sapwood is the \( n \)th ring counted inward from the last ring provided there are \( n \) living whorls in the crown (Fig. 2). A whorl in the model was considered to be a living one if it had at least one living twig.

To conclude, the general algorithm of the model is shown in Fig. 3. The diagram presented contains the simulation of light-dependent growth of twigs from Fig. 1 as an integrated part. The model was written in IBM PASCAL.

3. Results and discussion

To study the properties of the model developed we conducted a number of simulation experiments:
1. growth of a solitary tree;
2. growth of four trees in a dense clump;
3. growth of a suppressed tree after release;
4. growth of trees with different rates of twig removal.

The number of computing steps was 14 to 24, which was determined by the abilities of the current version of the computer program.

3.1. Growth of solitary tree and of trees in dense clump

The model tree growing freely without any impact from other trees presents a kind of reference point to compare with the results of other simulation experiments. The model gives rather linear growth of both height and diameter of the tree over the period of 1–20 years (Fig. 4). The imbalance between the reproduction of twigs and the sapwood area appears as early as at the age of 6 years, with the imbalance being equal to
0.75. The value means that the size of sapwood allows 0.75 times smaller mass of needles than that at the beginning of the step of growth. From that time, slight oscillations of the growth take place. The oscillations originate from the disproportion between the density of twigs and the area of the sapwood of the stem cross-section.

By a clump of model trees in the simulation experiment we mean four trees planted in the following way. A tree (no. 1) was put in the center of the clump, with the other three trees surrounding the former at a distance of 0.4 m from the center. The results of the height and diameter growth as compared with the growth of the open-grown tree are shown in Fig. 5.

There are a number of features of the growth which can be derived from the curves. Trees growing at the edge of the clump have a constantly higher height increment than the open-grown tree. The terminal shoot (as all others) of the model tree is subjected to the imbalance between the cross-sectional area and the amount of needles in the crown. The cause of the faster height growth is that the foliage-stem imbalance is much less severe in these trees. The value of the imbalance rarely drops below 0.87. At the same time, the diameter growth of a model tree is largely dependent on the density of twigs that determine the influence (S) to the stem circumference. Because the density of twigs in the clump-growing model trees is sufficiently lower than in the open-grown tree, the diameter growth in the clump trees is also much lower (Fig. 5B).

The model tree in the center of the clump presents another type of dynamics. The height growth of the tree is also faster than the growth of the open-grown tree but it has a very slow diameter growth. That is why there is a heavy imbalance between the sapwood area and the density of twigs since the age of 9 years. The imbalance at 9 years was 0.68, and further the tree could keep up the sapwood-needles balance only at the expense of a constant loss of twigs. By the age of 14 it practically stopped growing (Fig. 5). Therefore, the model tree had been “outcompeted” by the neighboring model trees and was at the point of “dying”. “Death” here means that the individual parameters of the model tree (increment, number of twigs etc.) are such that they correspond to dying off in real trees.

3.2. Growth of tree released after a long suppression

This simulation experiment presents other types of environmental impact on the tree growth. There are no definite competitors in this case to throw shadows to various parts of the model tree. Instead, there is a uniform worsening of conditions all over the tree crown (suppression). The suppression condition was achieved by assuming that the basic illumination is 0.41 times less intensive than the full illumination.

The growth of the suppressed tree was computed during 23 steps. In another part of the experiment, the suppressed tree was subjected to the conditions of open growth after the age of 15 years (time of release). The growth of the released tree was also computed up to 23 years.

Fig. 6 shows the results of the height and diameter growth of the suppressed and released model trees as compared with the growth of the open-grown model tree. The open-grown tree constantly overgrows the experiment trees with respect to both height and diameter. The release changes nothing in the situation, with the height seeming to be completely insensitive to the release. The diameter growth reacts more quickly to the release but the difference between the released and the open-grown tree is too big for

![Fig. 6. Height (A) and diameter (B) growth of the model trees: f, open-grown tree; s, suppressed tree; r, released tree; tr, time of release.](image-url)
the former to approach the diameter of the open-grown tree.

The cause of the low sensitivity of the growth to release is the disproportion between stem size and crown size. When the tree is released the twig density increases sharply. However, the small stem can not support such an amount of needles, which leads to a very heavy foliage–sapwood imbalance in the released tree. The imbalance is equal to 0.55 at step 17.

As a result, though the released tree may look as having more twigs (a “greener” view, Fig. 7) it actually can not stop stagnating because of the structural disproportions that originate from being suppressed too long.

3.3. Grazing effect on growth of trees

By grazing we mean here a removal of a constant proportion of the twigs at every growth step. The removed twigs are uniformly distributed over the whole crown. Two degrees of the removal were imposed on the trees in this experiment. Half (50%) of the twigs in one model tree was being removed every year of growth, another tree was annually grazed by 71% of all twigs. It should be noted that the grazing was done in such a way that the terminal twig was left intact. The growth of the trees was computed up to 24 years.

The grazing effect on the height growth of the model trees is similar to the effect of shading from sides because there is an increased mortality of the lateral twigs in both cases. The grazed model trees have a visibly faster height growth than the open-grown tree independently of the degree of grazing (Fig. 8A). At the same time, the degree of grazing strongly influences the diameter growth. The moderately (50%) grazed tree has a rather low diameter growth (Fig. 8B) which does not, however, differ dramatically from the diameter growth of the open-grown model tree. The heavily grazed tree (71%) has a constantly declining diameter growth. By the age of 24 years it has one twig only and no chance to survive.

4. Conclusions

The aim of the study was to create a simulative algorithm that would be able to reproduce a number of important features of real growth of Scots pine. In particular, the model pine tree should naturally react to neighboring model trees, their parameters and spacing. The empirical algorithm developed in this paper involves the internal processes of a tree in terms of correlations leaving apart subtle mechanisms of the biological resource movement.

We based our assessment of the model’s performance primarily on the general understanding of how a real tree is expected to react to the conditions of mutual growth or other factors.

From this point of view, we can conclude that
the model developed qualitatively reproduces a number of growth reactions of real trees:
1. growth in the stand and the grazing of twigs lead to a higher height growth and a lower diameter growth in comparison with the open-grown model tree;
2. a tree suppressed for a sufficiently long time is not sensitive to better conditions of growth which appear as a result of the release;
3. diameter growth is much more sensitive to various short-term environmental factors (suppression, release, grazing).

Moreover, the sizes of the model pine tree fall within reasonable limits of real sizes of a pine at the age range up to 20 years.

The model can be linked to models of global change. The environmentally sensitive unit of the model is the extension of the bud into the shoot (Table 1, nos. 5–9). The extension may be experimentally connected to a number of environmental factors (temperature, concentration of pollutants etc.) that limit the growth.

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