DYNAMICS OF UNEVEN-AGED STANDS OF NORWAY SPRUCE: A MODEL APPROACH

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The study presents the dynamics of uneven-aged Norway spruce (*Picea abies* (L.) Karst.) stands. The analysis of the stand dynamics is based on the theory of disturbances and patch dynamics. The stand dynamics is described using a transition matrix model. The effect of the spatial distribution on the growth of a Norway spruce stand is analyzed. In simulation studies the growth of the model stands clearly decreased with clustering, the maximum decrease was 40 % from the most regular pattern. The effect of the regeneration on the future development of an uneven-aged Norway spruce stand is studied. The calculations showed the primary importance of the ingrowth to the structure of an uneven-aged stand. Finally the empirical parameters were estimated for the transition matrix model. The transition probabilities were based on 48 study plots and the regeneration parameters on 8 study plots in eastern Finland (about 62°N, 30°E, 100-120 m asl.). The simulations showed that the sustainable harvest proportion of 5 years varies between 7 and 20 % depending on the stand basal area. The variations of thinning interval and intensity showed the thinnings should be done often and modest. The extension of the thinning interval from 5 to 10 years reduced the total removal slightly.

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CONTENTS

ORIGINAL PUBLICATIONS (I-IV)

ACKNOWLEDGEMENTS

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LIST OF ORIGINAL PAPERS

This thesis consists of a summary and four articles, in the text they are referred by their Roman numerals:

I Pukkala. T. & Kolström, T. 1988. Simulation of the development of Norway spruce stands using a transition matrix. For. Ecol. Manage. 25:255-267.

II Pukkala, T. & Kolström, T. 1991. Effect of spatial pattern of trees on the growth of a Norway spruce stand. A simulation model. Tiivistelmä: Tilajärjestyksen vaikutus kuusikon kasvuun. Simulointimalli. Silva Fenn. 25(3):117-131.

III Kolström, T. 1992. The role of ingrowth in sustaining the structure of an uneven-aged Norway spruce stand. Submitted manuscript.

IV Kolström, T. 1992. Modelling the development of an uneven-aged Norway spruce stand. Submitted manuscript.

In studies I and II, all the stages were done jointly by the authors except that T. Pukkala alone was responsible of computer programming and T. Kolström of field measurements.

1 INTRODUCTION

According to Baker (1934) "*uneven-aged stands* are stands that contain trees of every age, from seedlings of the current year to trees as old as rotation age". *Even-aged stands* are "stands in which all of the trees are the same age, arising from the germination or sprouting of one single year". These are strict definitions (Daniel et al. 1979). The concept *all-aged* is often used instead of uneven-aged. Also the concept *all-sized stands* is commonly used instead of uneven-aged stands.

In practice, the concept of an even-aged stand is often applied to forests that show a clearly defined, regular canopy without direct determination of ages at all (Baker 1934). The forest having a full assortment of size classes and the smallest trees most numerous is generally called uneven-aged (Baker 1934). Oliver and Larson (1990) referred the concept of *single-cohort* stands instead of even-aged stands and the concept of *multicohort* stand instead of uneven-aged or all-aged stands. In this paper the concept of a multicohort stand is understood as an uneven-aged stand having trees of all age classes, i.e., an all-aged stand. The concept of an uneven-aged stand is used as a synonym to a multicohort stand.

The selection management in silviculture arises from uneven-aged stands and the concept of selection forestry is used in this connection. Selection forestry has a long tradition in Central Europe (see e.g. Mitscherlich 1961, Kramer 1980, Dengler 1982, Kramer et al. 1988) and North America (see e.g. Baker 1934, Duerr and Bond 1952, Smith 1962, Trimble 1970, Halkett 1984). In Europe the research of uneven-aged stands is concentrated more on empirical field studies (see e.g. Burger 1952, Mitscherlich 1961, Pretzsch 1985, Spiecker 1986, Lundqvist 1989) with the main interest in *yield* comparisons with even-aged stands (see e.g. Kern 1966, Assmann 1970, Vuokila 1970, 1977).

The American researchers have been more interested in studying the stand

dynamics of uneven-aged stands (see e.g. Leak and Filip 1975, Larson 1982, Temple et al. 1987, Oliver and Larson 1990), *structure* of uneven-aged stands (see e.g. Buell 1945, Meyer 1952, Bruner and Moser 1973, Guldin and Baker 1988, Larsen 1991), and *management* of uneven-aged stands (see e.g. Davis 1966, Alexander 1986a, 1986b, Haight and Getz 1987a, Kaya and Buongiorno 1989, Haight and Monserud 1990). Some yield comparisons between even-aged and uneven-aged stands have been done also in America (see e.g. Hasse and Ek 1981, Haight and Getz 1987b).

The different cutting methods in uneven-aged silviculture are single-tree selection, group selection, and patch selection (Leak and Filip 1975, Guldin 1988, Matthews 1989). Single-tree selection consists of removing individual trees isolated from one another. Group-selection consists of removing trees in groups of a few to many trees. In patch selection trees are removed from a fixed small areas.

The silviculture tends to mimic natural stand development as closely as reasonable. Closer silviculture is to natural stand dynamics the lower the costs of silviculture are. The development of a stand can be expedited or retarded by various silvicultural methods, but its course cannot be changed (Kalela 1949). Knowledge of the stand structure and dynamics is useful in solving this problem (Larsen 1991).

Meyer et al. (1961) defined uneven-aged silviculture (Fig. 1) as the manipulation of the forest to maintain a continuous high standing crop, to provide regeneration of desired species, and to provide controlled growth and development of trees through a range of diameter classes. The regeneration dynamics is the major limitation of uneven-aged silviculture (Guldin 1988). According to Halkett (1984) to facilitate the use of uneven-aged silviculture, the following three requirements need to be set, i.e., a residual stocking goal, a diameter distribution goal, and a maximum tree size goal.

The requirement of appropriate residual stocking level is an important requirement that must be maintained to provide acceptable growth and yield. A residual stocking goal can be expressed by number of stems and basal area by diameter class. A diameter distribution goal is needed for regeneration, survival, and development of replacement trees (Halkett 1984). A maximum tree size goal states the upper end of the diameter distribution.

For some practical considerations uneven-aged silviculture and management are often regarded more complex than even-aged silviculture and management (Halkett 1984). Even-aged management systems are easier to plan and implement than uneven-aged ones. There are some aspects which encourage the use even-aged systems (Halkett 1984): opportunities exist for using labour-saving techniques in cuttings, the opportunity exists for introducing genetically improved tree stocks, and information systems of management are relatively straightforward.
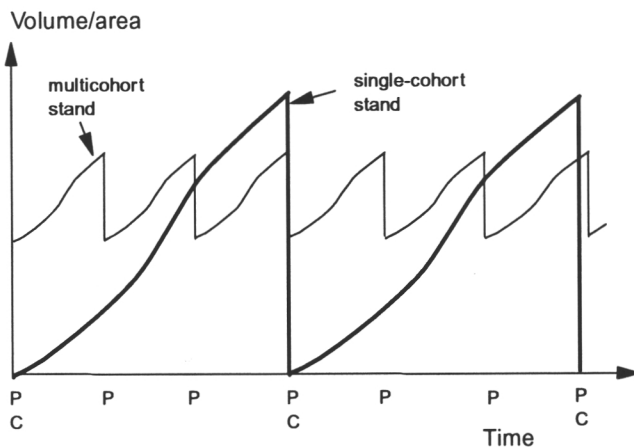
Figure 1. Schematic comparison of standing crops in even-aged and uneven-aged stands. Thinnings of uneven-aged stands occur at times *P* and even-aged stands at *C* (Redrawn from Oliver and Larson 1990).

A simulation model provides a useful tool for studying the development of a stand as well as the consequencies of different stand treatments. Transition matrix model is a population model suitable for forest management (Leslie 1945, Usher 1971). It is attractive because of the simplicity of interpretation and use and it is well suited to selection forestry, i.e., every diameter class can be treated separately. The transition matrix model was first used in forest management by Usher (1966, 1969a, 1969b) and later for example Buongiorno and Michie (1980), Rottier (1984), Boothby and Buongiorno 1985, Mendoza and Setyarso (1986), Sallnäs (1990), and Osho (1991). In the transition matrix models the stand dynamics is described by a single matrix (Jeffers 1982, Swartzman and Kaluzny 1987).

The aim of this work is to study the dynamics of an uneven-aged Norway spruce (*Picea abies* (L.) Karst.) stand. The stand dynamics is described using a transition matrix model. The general framework of modelling is presented is paper I. The growth of a stand and the recruitment of new seedlings are studied separately in papers II and III, respectively. In paper IV the transition matrix model is developed further with empirical background.

2 STAND DYNAMICS

2.1 The role of disturbances

Oliver and Larson (1990) state that "*stand development* is the part of stand dynamics concerned with changes in stand structure over time". They also state that "*forest stand dynamics* is the study of changes in forest stand structure with time, including stand behaviour during and after disturbances". According to White and Pickett (1985) *disturbances* are any relatively discrete events that disrupt the stand structure and/or change in the resource availability of the physical environment. There is no difference in the response of a tree to natural or human caused disturbances if the type of disturbance is same.

The broad framework for study and theory of disturbance is *patch dynamics* (Pickett and Thompson, 1978). For this Pickett and Thompson (1978) had three important points:
1. *Patch* implies a relatively discrete spatial pattern, but does not establish any constraint on patch size, internal homogeneity, or discreteness.
2. *Patch* implies a relationship of one patch to another in space and to the surrounding, unaffected or less affected matrix.
3. *Patch dynamics* emphasizes patch change.
A similiar concept to *patch dynamics* is *shifting mosaic* (see e.g. Bormann and Likens 1979) or *gap dynamics* (see e.g. West et al. 1981, Shugart 1984).

Natural forest communities are composed of a mosaic of patches in different stages of successional maturity (Whitmore 1978, Runkle 1985, Prentice and Leemans 1990, Leemans 1992). Watt (1947) interpreted forest mosaics as a spatiotemporal patterning of phases linked in regular cyclic succession. Each gap had its origin as a canopy gap formed by a local disturbance such as tree falls (Leemans and Prentice 1987, Shugart 1992). The rate and recovery process of gap formation and replacement are governed by the pattern of a forest disturbance (West et al. 1981, Runkle 1982, 1990).

The most profound effect on forest development is disturbances since they kill
vegetation and thus release growing space. Disturbances make it possible for
new trees and other plant species to occupy the released growing space (Runkle
1981, Oliver and Larson 1990, Kellomäki 1991).

Disturbances can be described by their frequency, distribution, return interval,
area covered, magnitude, and other factors (White and Pickett 1985).
According to the amount of overstorey removed, disturbances can be divided
into major and minor disturbances (Oliver 1981). Major disturbances remove or
kill existing trees above the forest floor vegetation (stand-replacing
disturbances). Minor disturbances leave part of the predisturbance trees alive.
Logging is similiar to disturbance caused by windthrow in that cutting of trees
remove the overstorey and release the understorey (Spurr and Barnes 1980).

Trees respond to disturbance depending on the characteristics of the species and
disturbance. Major disturbances produce even-aged stands, since all component
trees have been assumed to regenerate shortly after the disturbance (Oliver and
Larson 1990). Minor disturbances change the growing space of trees surviving
in minor disturbances. Uneven-aged stands or all-aged stands are the result of
two or more minor disturbances. Both minor and major disturbances give
different species a competitive advantage in regeneration. Thus, the
silviculturist can greatly influence subsequent forest composition and the rate of
succession by regulating the intensity and pattern of logging (Spurr and Barnes
1980).

2.2 Stand development

The dynamic biological systems consist of the processes growth, death, and
replacement (White and Pickett 1985). Oliver and Larson (1990) mentioned
stand initiation stage and reinitiation stage. Shugart (1984) used birth instead of
replacement. The regenerative properties of tree species and the characteristics

of the disturbance define the possibilities for a new individual to enter the stand. The surviving trees and new initials compete for the growing space released after the disturbance.

Shugart (1984) classified tree species successional roles according to their relations to gap size in regeneration and mature tree mortality (Fig. 2). Role 1 tree species require large gaps for regeneration. They grow rapidly to a large size and produce large gaps after the death. Role 2 species do not require gaps for regeneration. They are shade-tolerant but they grow at a reasonable rate to large size producing a large gap after death.

Mature tree mortality

	produces gap	doesn't produce gap
require gap	Role 1	Role 3
doesn't require gap	Role 2	Role 4
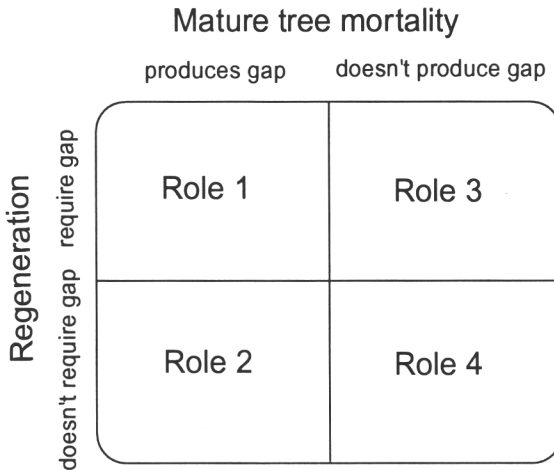
(Regeneration)

Figure 2. The role of gap-requiring and gap-producing tree life history traits (Redrawn from Shugart 1984).

Role 3 species require gaps for regeneration. They grow rapidly, but the time-span is short. Thus, they do not produce gaps upon their death. Role 4 tree species do not require gaps for regeneration. They are small and do not produce gaps upon their death. Kellomäki (1991) classified Norway spruce (*Picea abies* (L.) Karst.) to be tree species of the role 2. Prentice and Leemans (1990) proposed Norway spruce to be probably tree species of the role 1. Norway spruce is a shade-tolerant tree species as well as growing into a large

size and producing a gap upon the death.

A minor disturbance creates a new cohort composed of new seedlings. This minor disturbance has to be so severe that it can release enough growing space to allow a new cohort of trees to grow as a major component of the stand (Hibbs 1982, Oliver and Larson 1990). New stems invade small openings in the stand after disturbances to groups, or patches, of overstorey trees (Runkle 1981, 1982). These younger trees become suppressed until they are again released by small disturbances and finally they reach the overstorey (Kalela 1949). Actually many repeated small disturbances create a mosaics of small single-cohort stands, which appear as a multicohort stand.

This stand initiation stage is naturally not so ideal. If surviving trees are vigourous and expand quickly, the invading or surviving new cohort of seedlings is suppressed or killed. Trees do not all invade the disturbed area in a single year. Another part of new trees come as understorey reinitiation (see e.g. Schmidt-Vogt 1986) as the case is with role 2 species like Norway spruce. The behaviour of stand components after each minor disturbance determines the further development of a multicohort stand. Frequent, small disturbances can create all-aged stands if successive disturbances occur while trees are still initiating from the previous disturbance (Oliver and Larson 1990).

In idealized development of a multicohort stand all disturbances occur at similar time intervals, allow the same species to initiate, and create uniform spatial distribution of regeneration (Fig. 3). In each disturbance the same proportion of trees are removed in each cohort and the remaining ones are evenly spaced (Oliver and Larson 1990). Disturbances (cuttings) remove the oldest cohort, reduce the number of trees in other cohorts, release growing space, promote new cohorts, and increase the growth in existing trees. All trees except those in the oldest cohort are supressed (Larson 1982).

In a multicohort stand there are present all the stages of a single-cohort stand.

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They are all in competition with each other. Numbers of trees in a multicohort stand and the tree invasion pattern and subsequent distributions of age cohorts reflect the disturbance and mortality patterns and site characteristics (Oliver and Larson 1990).
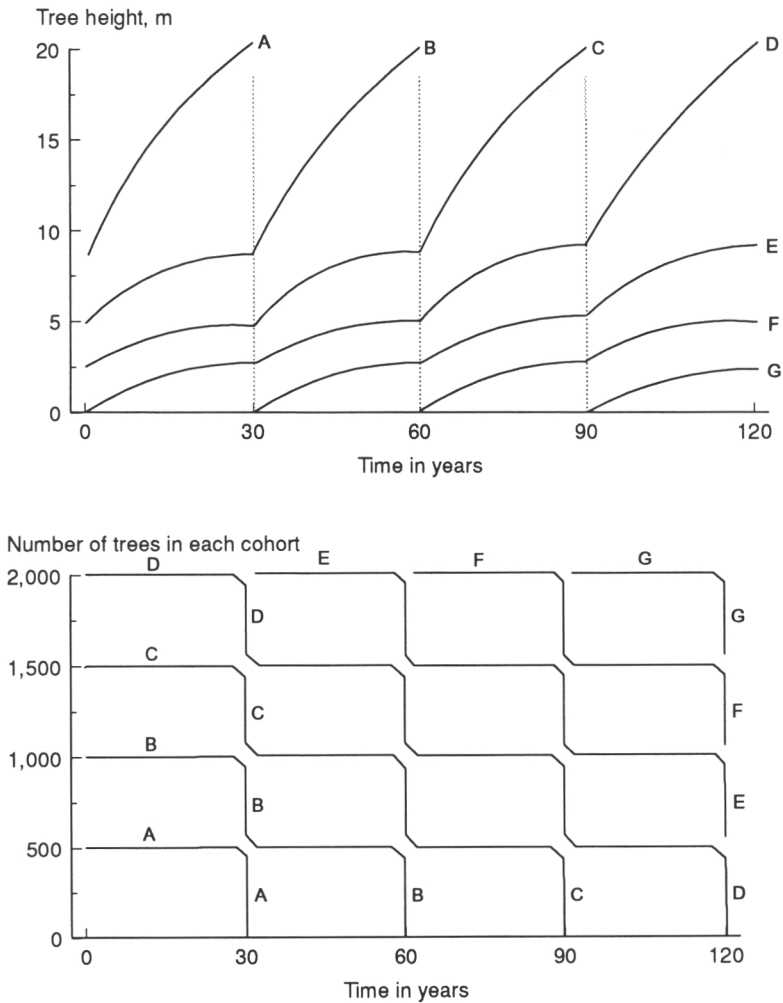
Figure 3. Idealized development of a multicohort stand with cohorts evenly distributed in time. Individual cohorts are identified *A* through *G*. The thinning interval is 30 years (Redrawn from Oliver and Larson 1990).

In selection forestry thinnings are acting as disturbances. Thus, the behaviour of a multicohort stand after disturbances gives the idea for thinning intensity. Thinning where dominant trees are removed favours establishment of a new cohort. Thinnings from below favour dominant and codominant trees more than trees in lower classes or a new cohort (Oliver and Murray 1983).

2.3 Structure of uneven-aged stand

Idealized development of an all-aged stand results a reverse J-shaped diameter distribution (Fig. 4). Trees in a new cohort are growing at first similarly. The competition from other trees in the same cohort as well as other cohorts differentiates slowly the development of trees in a cohort. Thus there will be a diameter distribution for each age class. These diameter distributions form together the reverse J-shaped diameter distribution of a multicohort stand.
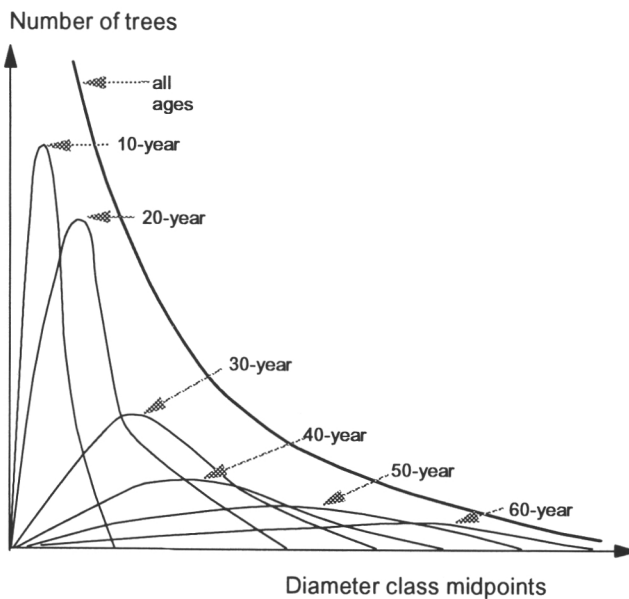
Figure 4. Idealized reverse J-shaped diameter distribution of tree ages in multicohort stand. (Redrawn from Oliver and Larson 1990).

A reverse J-shaped distribution can be described for example as a negative exponent function (Meyer 1952, Pretzsch 1985), a polynomial function (Hett 1971) or a Weibull distribution (Bailey and Dell 1973). However, the most usual is the q-value. The French forester Liocourt found that a sustainable diameter distribution is characterized by a constant quotient called q-value. It gives the ratio of the number of trees in successive diameter classes (Meyer 1952). This relationship generates a geometric series of the form:

$$a,\ aq,\ aq^2,\ aq^3\ ...$$

where a is the number of trees in the largest diameter class and q is the ratio of geometric series. The q-value tells the increase in the number of trees as diameter decreases. Thus it is a fundamental characteristic of the uneven-aged condition (Halkett 1984).

The q-values ranging between 1.3 and 2.0 have been recommended for different management situations (Halkett 1984). Alexander and Edminster (1977) found the q-value of 1.6 to have been the most typical in spruce-fir stands. Leak and Filip (1975) preferred the q-value of 1.8 in hardwoods of New England.

Trees in a multicohort stand do not begin growing at a uniform spacing due to the disturbances. Thus, most trees begin in aggregated patterns with the area of disturbance containing most of seedlings and some areas containing no individuals (Daniels 1978, Horn 1981). The spatial distribution of advance regeneration, stumps and roots for sprouting, suitable seedbeds for germination, competition from other plants, behaviour of the disturbance, and other factors cause the initial spatial pattern (Oliver and Larson 1990, Pukkala and Kolström 1992). Later the results of inter- and intraspecific competition affect the spatial pattern and thus the mortality of trees. Mortality is a very important factor in determining stand development patterns (Daniels 1978, Kenkel et al. 1989). It affects the competition between trees.

3 THE REVIEWED STUDIES

The first paper (I) presented the basics of the transition matrix model. In a transition matrix model the three basic processes of a stand (birth, growth, and death) are presented in one matrix. The presented transition matrix model was applied to Norway spruce (*Picea abies* (L.) Karst.) selection forest. The transition matrix model was further developed by adding a separate waiting class for small seedlings to describe the dynamics of them. Simulations showed the lack of sensitivity of selection forest to small changes in management as well as for small errors in model parameters. The model in this paper had a rather poor empirical background.

The second paper (II) concentrated in analysing the effect of the spatial distribution on the growth of a Norway spruce stand. First, a method to generate theoretical Norway spruce stands was presented. Second, a spatial growth model was presented to predict the growth of these stands. The stand generation procedure first predicted the tree diameters from a few stand parameters and from tree locations. Tree age and height were predicted using spatial models. Diameter growth and basal area growth were predicted in growth models. Past growth was used in one pair of the models. In simulation studies the growth of the model stands clearly decreased with clustering, the maximum decrease was 40 % from the most regular pattern.

The third paper (III) analyzed theoretically the effect of the regeneration on future development of an uneven-aged Norway spruce stand. Two different model types were used in calculating the required ingrowth to sustain the uneven-aged structure of a stand. The model types used were a transition matrix model and a process-oriented gap model. The ingrowth in the transition matrix model was based on the size of the removed tree and the basal area of the stand. In the gap model the ingrowth was a result of number of seedlings and environmental conditions. The used gap size (100 m^2) of the gap model proved to be too small to be used with selection forestry. The thinnings of

large diameter classes were applied unproperly because there are only a few large trees in the simulated gap when the harvest proportion is between 5 and 20 % from the number of stems in each diameter class. The calculations showed the primary importance of the ingrowth to the structure of an uneven-aged stand.

In the fourth (IV) paper the empirical parameters were estimated for the transition matrix model presented in the first paper (I). The transition probabilities were based on 48 study plots and the regeneration parameters on 8 study plots in eastern Finland (about 62°N, 30°E, 100-120 m asl.). The simulations showed that the sustainable harvest proportion of 5 years varies between 7 and 20 % depending on the stand basal area. The shape of the diameter distribution had no effect on the sustainable harvest proportion. The variations of thinning interval and intensity showed the thinnings should be done frequently and modestly. The extension of the thinning interval from 5 to 10 years reduced the total removal slightly.

4 CONCLUDING REMARKS

The understanding of the forest stand dynamics is essential for the management of both even-aged and uneven-aged stands. This point of view is emphasized especially in the selection forestry where the three basic processes (birth, growth, and death) of the stand dynamics are running simultaneously (I, IV). The knowledge of the stand dynamics aids in understanding the future stand structures and development patterns (Oliver and Larson 1990, Larsen 1991). This future development may be slowed or quickened by minor disturbances like cuttings but it does not change its course. Thus, the target structure should be planned from the ecological characteristics of tree species (Kalela 1949).

The uneven-aged structure of a stand is a result of *autogenic succession* (Kellomäki 1991) or *initial floristics* development pattern (Oliver and Larson 1990). These development patterns presuppose a shade-tolerant tree species capable to regenerate below the overstorey, i.e., role 2 and 4 tree species in the classification of Shugart (1984) (see Fig. 2). Norway spruce is a climax tree species and regenerates below overstorey (see e.g. Sarvas 1944, Kalela 1949).

The Norway spruce seedlings of the understorey grow quite vigorously after release (Sarvas 1944). According to Kalela (1949) the establishment and initial development of the seedlings must be helped with frequent cuttings. These cuttings should remove trees of the lower crown layer because the lower crown layers are the greatest obstacles to the regeneration of new dominants.

The transition matrix model is originally based on the assumption that a gap is needed for regeneration (I). This assumption is moderated by allowing some regeneration below overstorey (IV). Thus, this modelling approach fulfills the requirements of the regeneration represented by the behaviour of stand dynamics of Norway spruce. The idea of minor disturbances in patch dynamics corresponds frequent thinnings.

Uneven-aged silviculture, involving the cutting of individual trees of small groups of trees, simulates natural minor disturbances such as might result from the death or windthrow of larger trees (Halkett 1984). Stronger disturbances correspond to the idea of patch selection where trees are removed from a fixed small areas. Major disturbances are similiar to clearcuttings and thus, near the management of even-aged stands.

The strength of disturbances can be seen as a question of the scale. In this way the different silvicultural systems can be seen based on the scale. Uneven-aged silviculture is small scale forestry and even-aged silviculture is large scale forestry. The main difference between these two methods of silviculture is this scale, i.e., the amount of area we are interested in at one time (see also Mikola 1984).

Transition matrix models can be used from small areas (see e.g. I, Buongiorno and Michie 1980, Haight et al. 1985) up to large areas (see e.g. Mendoza and Setyarso 1986, Sallnäs 1990). On the basis of these ideas the model approach used in this study corresponds to the stand dynamics based on disturbances.

The stochasticity in the natural regeneration of Norway spruce is wide (IV, Leinonen et al. 1989). One reason is the wide variation in the flowering and seed crop of Norway spruce (Koski and Tallqvist, 1978). The emergence and initial development also play an important role (Yli-Vakkuri 1961a, 1961b). Nevertheless, the regeneration creates the basic layout for the stand structure (III).

At later phases the competition in the stand defines the growth and mortality of the new cohort. In understanding the competition of a stand the spatial distribution of the stand has an essential role (II). The transition matrix model does not consider the spatial distribution of a stand. The spatial pattern is also needed for the forest management like selection of trees to be thinned.

The lack of knowledge about the natural regeneration and the initial development of a new cohort is substantial (III, IV). This area requires a lot of work to be done in the future. First the future modelling efforts need to take into consideration the stochasticity of the regeneration. Second area to be noticed is the spatial pattern of the regeneration and the stand development. Third area to go on is the effect of the mixture of tree species on the dynamics of uneven-aged stands.

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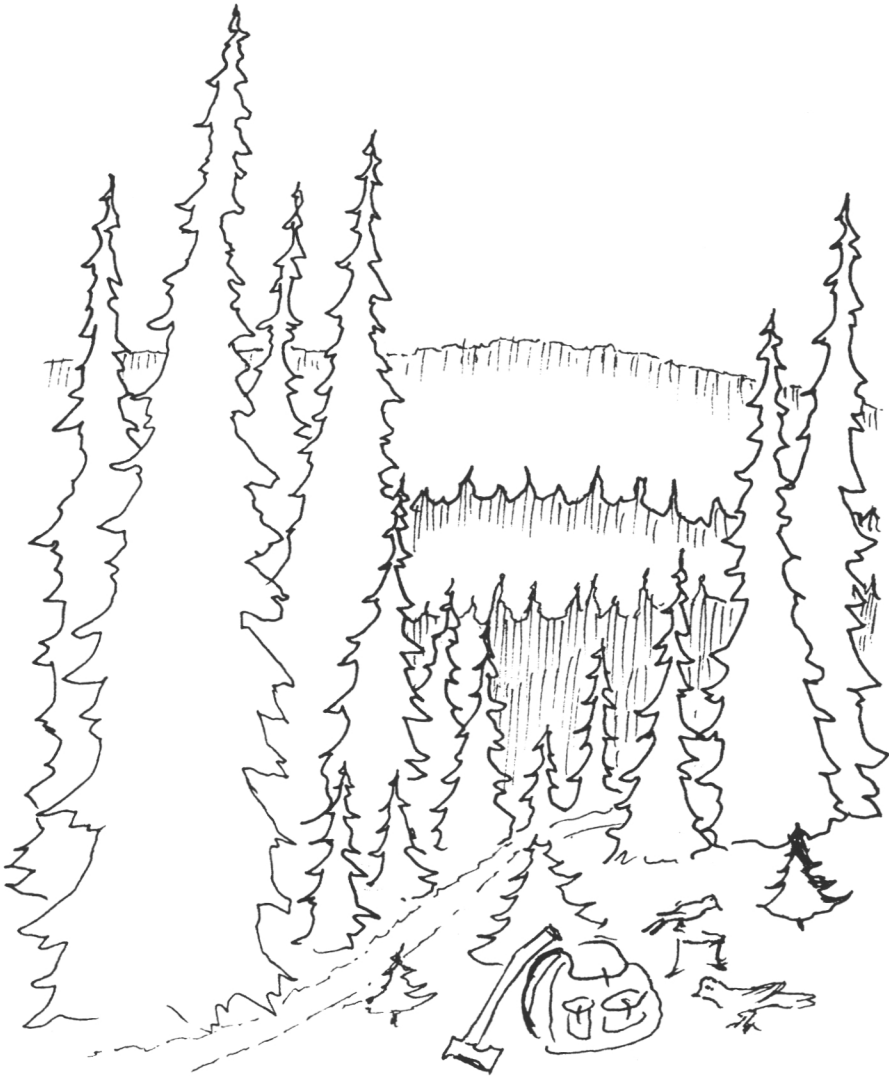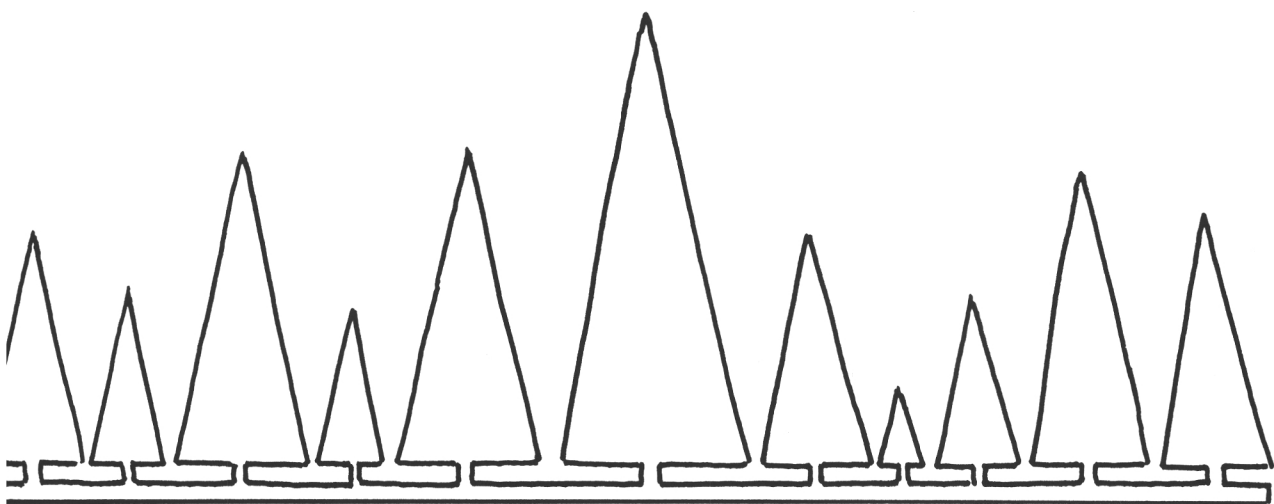
Simulation of the Development of Norway Spruce Stands using a Transition Matrix

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ABSTRACT

Pukkala, T. and Kolström, T., 1988. Simulation of the development of Norway spruce stands using a transition matrix. *For. Ecol. Manage.*, 25: 255–267.

The transition-matrix model was applied to a Norway spruce selection forest grown under Finnish conditions. The transition probabilities depended on stand density according to a model which was estimated by using empirical single-tree growth models. The dynamics of small seedlings was modelled by adding a separate size class for them to the matrix model. A computer program with comprehensive output was prepared for making simulations. According to the simulations, the selection forest is insensitive to small changes in management and the model is insensitive to small errors in parameters. The volume production of a selection forest is inferior to that of an even-aged stand.

INTRODUCTION

A simulation model is a good tool for studying the consequences of different stand treatments. The simulations are usually carried out by growth models which are either treewise or standwise (Buongiorno and Michie, 1980). The benefit of using single-tree models is that the stand can be illustrated and the treatments simulated much more thoroughly than by stand models. The forecasts of the volume increment is, however, usually as accurate with stand models as with tree models (Ek and Monserud, 1979).

The simulation models used in forest management are usually based on empirical regression equations on birth, growth and mortality. Because the models are based on a limited amount of data, the simulated results may not always be realistic. Another approach is to rely on population models in forest management planning.

One population model suitable for forest management is the transition-matrix model (Leslie, 1945; Usher, 1971), which is best suited to selection forestry. The transition-matrix model was first used in forest management by

Usher (1966; 1969a) and later by Buongiorno and Michie (1980) and by Mendoza and Setyarso (1986), among others. In the later applications of the model, the growth of tree dimensions did not depend on stand density; this restricts the use of the models to a limited range of growing densities.

The aim of the present study was to prepare a preliminary transition-matrix model and simulation program for Norway spruce stands grown under Finnish conditions and managed using selection principle. The output of the program was aimed to be as comprehensive as the output from single-tree growth models. The resulting model was used for studying the dynamics of a selection forest.

TRANSITION MATRIX MODEL

The basic form of the transition matrix model is:

$$
\begin{vmatrix} h'_1 \\ h'_2 \\ h'_3 \\ \cdot \\ \cdot \\ \cdot \\ h'_n \end{vmatrix} = \begin{vmatrix} f_1 & f_2 & \cdots & f_n \\ p_1 & 0 & \cdots & 0 \\ 0 & p_2 & \cdots & 0 \\ \cdot & & & \\ \cdot & & & \\ 0 & 0 & \cdots & p_{n-1} \end{vmatrix} \cdot \begin{vmatrix} h_1 \\ h_2 \\ h_3 \\ \cdot \\ \cdot \\ \cdot \\ h_n \end{vmatrix} \tag{1}
$$

where $h_1...h_n$ and $h'_1...h'_n$ represent the frequencies of age classes at times t and $t+k$, respectively. In the matrix, f_i ($i = 1, 2, ...n$) refers to the fecundity of a female in the ith age class. Element p_i ($i = 1, 2, ...n-1$) is the probability that a female belonging to the ith age class will be alive after a definite time step.

The latent roots and latent vectors of the transition matrix satisfy the equation:

$$Aq = \lambda q \tag{2}$$

where: A is transition matrix; q = latent vector; and λ = latent root. If the population has an age-distribution corresponding to a latent vector, the latent root tells directly the rate of increase of the population. The harvest that keeps the population constant is $(\lambda-1)/\lambda$. If this proportion is cropped from every age class, the population remains unchanged and can be regarded as stable. It can be shown that the stable age-class distribution and the growth rate of the population are defined by the greatest latent root and the corresponding latent vector (Usher, 1969b, 1971).

In a transition-matrix model describing a selection forest, it is more practical to use size distribution (e.g. diameter distribution) instead of age-class distribution. This causes little change to the transition matrix, because during a given time-interval a tree can either enlarge to the next class or remain in the same class. In addition, the number of new seedlings correlates more with the

number of trees removed in thinnings rather than with the size and number of existing trees. Seedlings are born into the gaps left by removed trees; removal of a bigger tree means more seedlings. Hardly any seedlings will appear in the gap left by a removed small tree, because the neighboring trees usurp the space by becoming broader. The corresponding transition matrix model is (Usher 1969a):

$$
\begin{vmatrix} h'_1 \\ h'_2 \\ h'_3 \\ h'_4 \\ \cdot \\ \cdot \\ h'_n \end{vmatrix} = \begin{vmatrix} a_1 & c_2(\lambda-1) & c_3(\lambda-1) & ...c_n(\lambda-a_n) \\ b_1 & a_2 & 0 & ... & 0 \\ 0 & b_2 & a_3 & ... & 0 \\ 0 & 0 & b_3 & ... & 0 \\ & \cdot & & & \\ & \cdot & & & \\ 0 & 0 & 0 & ... & a_n \end{vmatrix} \cdot \begin{vmatrix} h_1 \\ h_2 \\ h_3 \\ h_4 \\ \cdot \\ \cdot \\ h_n \end{vmatrix} \qquad (3)
$$

In this model the element a_i ($i = 1, 2, ...n$) is the probability that a tree of the ith size class will remain in the same class and b_i ($i = 1, 2, ...n-1$) the probability that a tree will advance to a larger class. If the sum of elements a_i and b_i is less than 1, part of the trees belonging to the size class i will die during the growth period or move up two size-classes. The coefficient c_i gives the number of established trees born in the gap left by one tree removed from class i. Each size-class is supposed to be thinned according to the sustained harvest proportion $(\lambda-1)/\lambda$, once during every time interval. The element $(1,1)$ should be $a_1+c_1(\lambda-1)$, if new seedlings would come to the gaps left by trees removed from the smallest size-class.

SIMULATION MODEL

Model parameters

To obtain the transition probabilities dependent on stand density, the following procedure was applied:
(1) generate model stands with different densities;
(2) calculate the transition probabilities for the model stands by individual-tree growth models;
(3) use the results for a regression model that predicts how the transition probability depends on stand density in different diameter classes.
The data for constructing the regression model consisted of model stands of Norway spruce (*Picea abies* Karst.) with different basal areas (Table 1). The stands were generated by estimating the diameter distribution of stand basal area using the beta-function as a theoretical distribution.
To calculate the beta-distribution, it is necessary to know the minimum, maximum and variance of the distribution. The minimum was always taken

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TABLE 1

Characteristics of stands used as data in the calculation of transition probabilities

Basal area $(m^2\,ha^{-1})$	Mean diameter (cm)	Age (years)	Mean height (m)
5	21.5	95	20.1
10	22.0	100	20.8
15	22.5	105	21.5
20	23.0	110	22.2
25	23.5	115	22.9
30	24.0	120	23.6
35	24.5	125	24.3
40	25.0	130	25.0

The stand characteristics corresponding to basal area 40 m² ha⁻¹ are obtained from Yield Tables (Koivisto, 1954) made for natural spruce stands (good site, *Oxalis-Myrtillus* type). The rest of the stands were obtained by assuming that in sparse stands (low basal area) the trees are younger, the proportion of small trees higher and the tapering of trees greater than in old natural forest.
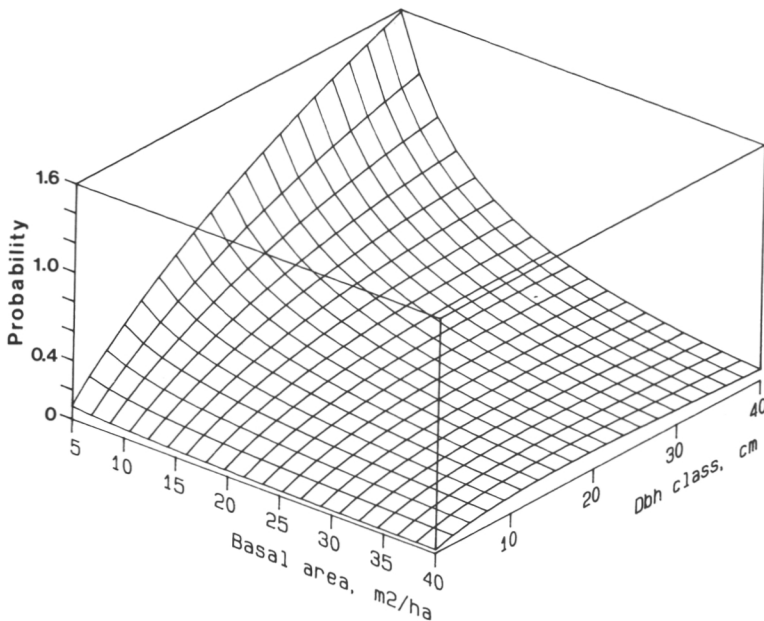

Fig. 1. Regression model of transition probability illustrated as a surface.

as 0 cm and the maximum as 40 cm. The variance was calculated by the empirical equation of Päivinen (1980). Using these characteristics and the tabulated mean (Table 1) the diameter distribution was derived by the method of Loetsch et al. (1973, p. 52).

For each model stand of Table 1, the basal area was calculated for 500 diameter classes of equal width. The basal areas were converted to number of stems (trees ha^{-1}) by dividing the basal area of the diameter class by the basal area of the class midpoint tree. The height of each class midpoint was needed as a predictor of the growth model and was estimated by Pukkala and Tahvanainen (1986) as:

$$h = 1.3 + C(d^2/(1.907+0.1672d)^2) \tag{4}$$

where h is height (m); d, diameter (cm); and C, correction factor to obtain the height presented in Table 1 for mean diameter.

For each class midpoint tree the diameter increment for the next 5-year period was estimated by the model of Nyyssönen and Mielikäinen (1978), after which the transition probabilities for 4-cm diameter classes were calculated. These probabilities and the basal areas of the model stands were used for calculating the following equation which gives the dependence of transition probability on stand density (Fig. 1):

$$b_i = \exp(0.8601\ln(d_i) - 0.5557\ln(G) - 0.0007226Gd_i - 2.113) \tag{5}$$

where b_i is the transition probability of class i; d_i is the midpoint of class i (cm); and G is stand basal area (m^2 ha^{-1}). The F-value of the equation is 197.5 (3,72), degree of determination 0.887 and standard error of estimate 0.2574.

The growth of small seedlings is very slow in an uneven-aged Norway spruce stand and the mortality of seedlings remarkably high. These features of the stand dynamics were taken into account with the help of the so-called 'waiting class'. The class was added to the matrix model for trees whose height is less than 1.3 m. The new seedlings wait for many years in this class before entering the first diameter class. The element b_1 is set to 0.1, i.e. 10% of small trees will grow up to the next size-class during the 5-year period. Element a_1 is taken as 0.5 which means that 50% of the plants remain in the same class; the remaining 40% will die. The values c_i of the transition matrix (Equation 5), which indicate how many new seedlings can appear to the gap left by one harvested tree, were taken as:

	Diameter class (cm; class midpoint)									
	2	6	10	14	18	22	26	30	34	38
Parameter c_1	0	0	1	3	5	9	15	22	30	40

Rather low values were used because it was assumed that the infilling by sur-

rounding trees will utilize the greatest part of the gap. In addition, the forest floor under Norway spruce trees consists commonly of raw humus which is very unfavorable for plant establishment.

Simulation program

A FORTRAN-program was designed in order to make simulations with the model. The program input consists of frequencies of ten 4-cm diameter classes representing diameters 0–3.999 cm, 4–7.999 cm, etc. These are the elements $h_2...h_{11}$ of the matrix model (Equation 3). The first element (h_1) is the frequency of trees whose height is less than 1.3 m and it is also entered into the program.

In the computations, each diameter class is represented by the basal area median tree (not class midpoint), the diameter of which is estimated by using the method of Loetsch et al. (1973, pp. 55–56). For each median tree a set of tree characteristics is calculated: height by Equation 4; and the total, sawlog and pulpwood volumes by the volume and taper equations of Laasasenaho (1982). The stand characteristics are obtained as sums or means of the tree characteristics.

The tree and stand characteristics are calculated after every growing and thinning period, i.e. every 5th year. The characteristics are calculated separately for standing and removed trees.

Before each growing period the transition matrix corresponding to the actual stand density is derived. The probabilities b_i $(i = 2,...11)$ are calculated by Equation (5) and the probabilities a_i as a difference $1-b_i$. The maximum latent root of the transition matrix is sought by Newton-Raphson technique using the equations of Usher (1969a). The stable proportions of diameter classes — or the latent vector corresponding to maximum latent root — are calculated by Usher (1966):

$$q_{i+1} = (b_i/(\lambda-b_{i+1}))q_i \quad i = 1,...10 \tag{6}$$

The values are scaled so that the sum of the frequencies $q_1...q_n$ equals the total number of trees ha^{-1} of the stand under simulation.

When the vector of the class frequencies is multiplied by the transition matrix, the diameter distribution 5 years later is obtained. After multiplication, the user of the program can harvest part of the trees. Trees whose diameter is over 40 cm are harvested automatically. The percentage removed may be the same in all diameter classes or it may vary. Before the next growing period several kinds of diagrams can be created by using the simulation program:
— computer drawing of the stand;
— diameter distribution of the stand;
— temporal development of stand characteristics (see Fig. 3);
— changes in diameter distribution of the stand (see Fig. 4).

The program output also includes a lot of numerical data:
— actual transition matrix;
— stable diameter distribution corresponding to the present stand basal area;
— summary of stand characteristics of the remaining and harvested trees.

SIMULATION EXAMPLES

In the first example, the dependence of the sustained-harvest proportion on the stand basal area is calculated for a stable selection forest (Fig. 2). In a sparse stand (basal area $< 10\,\mathrm{m^2\,ha^{-1}}$), 10% or more of the trees with diameter less than 40 cm can be harvested after each 5-year period (and all trees whose DBH is greater than 40 cm). In a very dense selection forest (basal area > 35 $\mathrm{m^2\,ha^{-1}}$) the sustained harvest is less than 4% of trees smaller than 40 cm. Because of the mutual dependency between productivity and stand density the removal is only about 50% greater with basal area $35\,\mathrm{m^2\,ha^{-1}}$ than with basal area $10\,\mathrm{m^2\,ha^{-1}}$.

In the second problem the effects of different proportions of removal in different diameter classes were evaluated. The initial situation in both examples was a stable stand with a density of 2735 trees $\mathrm{ha^{-1}}$ and the total basal area of $19.3\,\mathrm{m^2\,ha^{-1}}$ (Table 2).

When large trees (diameter > 20 cm) are harvested 20% more heavily than the sustained-harvest proportion, and small trees (diameter < 20 cm) 20% less heavily, the total volume of the stand increases and the removal decreases slowly during the 100-year simulation period (Fig. 3a) When small trees (di-
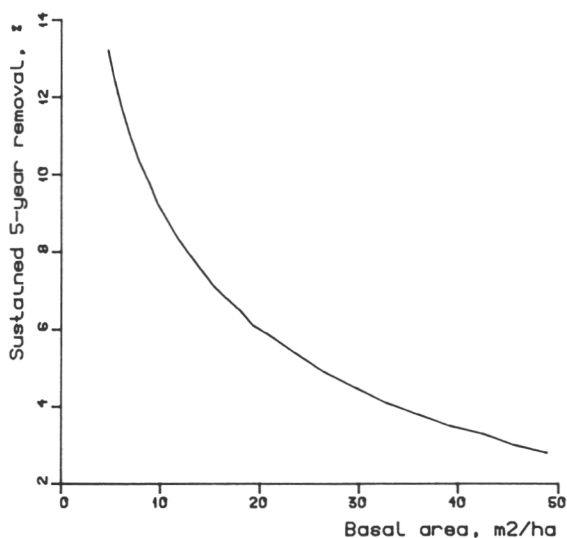

Fig. 2. Dependence of sustained removal proportion on basal area in a stable selection forest.

ameter < 20 cm) are harvested more heavily than large ones, the volume of the stand first increases and then decreases (Fig. 3b). The volume of removal also increases constantly. The effects of differentiated harvest proportions are very small and slow. In both cases the stand structure remains almost constant (Fig. 4). The removal is constant at about 20 m^3 ha^{-1} during each 5-year period, or 4 m^3 ha^{-1} $year^{-1}$.

The third simulation examined the change from an even-aged stand structure to a selection forest. In the first case the initial diameter of all trees is 10 cm and the stocking is 2000 trees ha^{-1}; in the second case the initial diameter is 30 cm and the stocking is 300 trees ha^{-1}. The stands were harvested every 5th year by removing all trees whose diameter is over 40 cm and cropping from smaller trees the sustained-harvest proportion corresponding to the actual stand basal area.

When the diameter is 10 cm at the beginning of the simulation, the stand

TABLE 2

Diameter distribution of stand used in simulation examples

Class midpoint (cm)	Number of trees ha^{-1}	Class midpoint (cm)	Number of trees ha^{-1}
2	682	22	64
6	322	26	48
10	188	30	38
14	123	34	30
18	86	38	24

Number of trees with height less than 1.3 m was 1129 trees ha^{-1}.
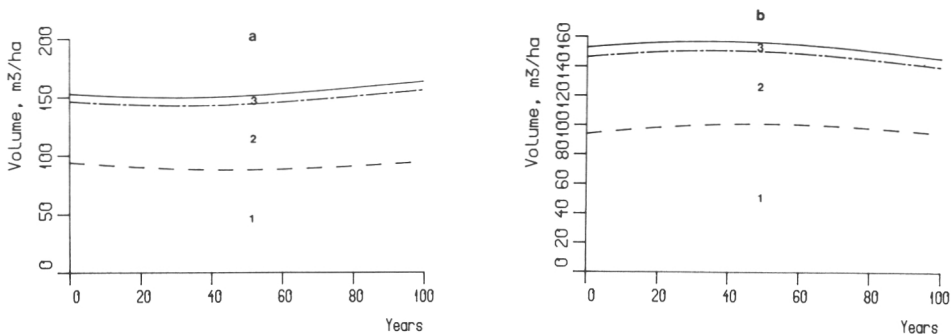
Fig. 3. Stand volume after cutting during the 100-year simulation period. a: removal of large trees (DBH > 20 cm) increased and removal of small trees (DBH < 20 cm) decreased by 20% from the sustained-harvest proportion; b: large tree removal decreased and small tree removal increased by 20%. 1 = sawlog, 2 = pulpwood, 3 = waste wood.
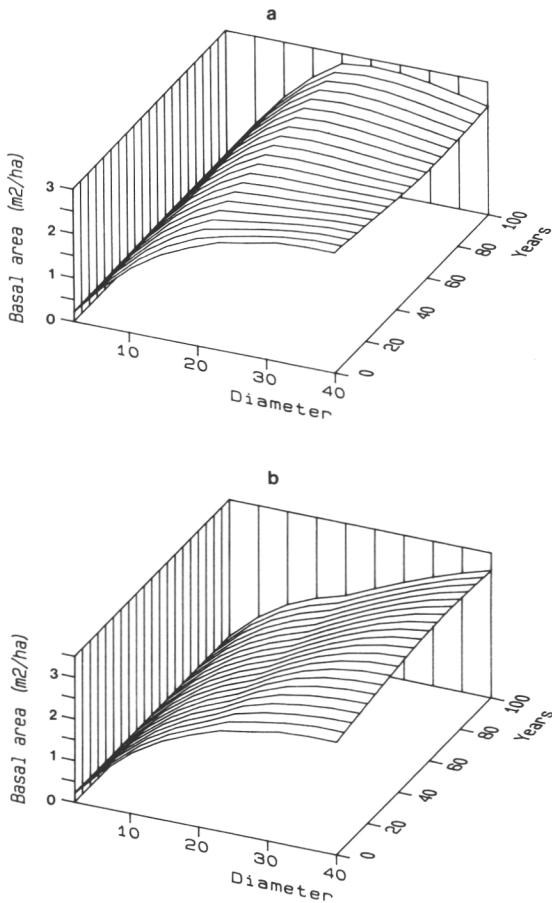
Fig. 4. Diameter distribution of basal area (m² ha⁻¹) during the 100-year simulation period. See Fig. 3 for explanations for a and b.

volume and removal increase for the whole 100-year period, as does the proportion of sawlog timber (Figs. 5a and 6a). When the initial stand diameter is 30 cm, the volume begins to fall because large trees are harvested and there are not enough rapidly growing young trees to compensate for the volume loss (Fig. 5b). The removal first increases but, when all trees of the original stand are harvested, it decreases to a very low level after about 50 years' simulation (Fig. 6b). The change from an even-aged stand structure to a selection forest takes a very long time-span, at least when the above-mentioned thinning practices are followed.

DISCUSSION

With a transition-matrix model it is possible to study the different treatment alternatives of a selection forest (Usher, 1966; Buongiorno and Michie, 1980;
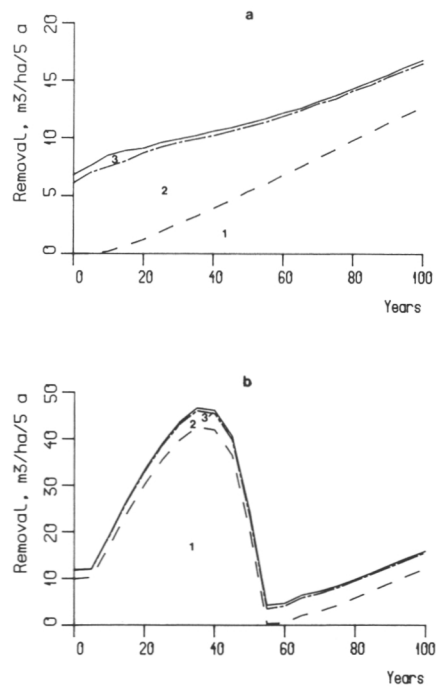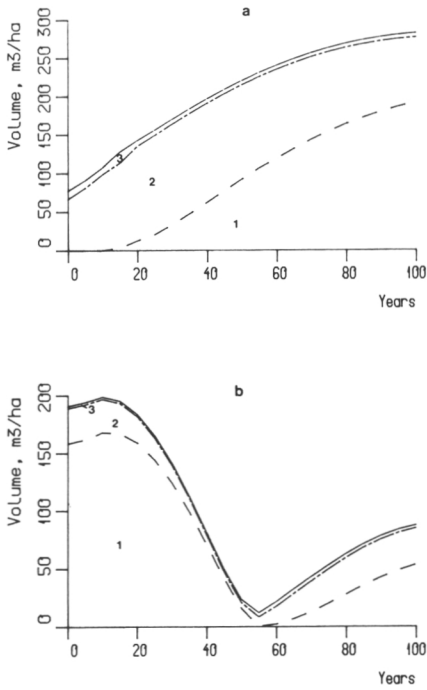
Fig. 5 (left). Stand volume after cutting during the 100-year simulation period when diameter of trees is 10 cm (a) or 30 cm (b) at the beginning of the simulation. 1 = sawlog, 2 = pulpwood, 3 = waste wood.

Fig. 6 (right). Removal of 5-year period during 100 years of simulation when the diameter of trees is 10 cm (a) or 30 cm (b) at the beginning of the simulation. 1 = sawlog, 2 = pulpwood, 3 = waste wood.

Mendoza and Setyarso, 1986). It helps the forest manager to find an optimal way to manage the forest or to compare the production of selection forests to that of stands managed under other systems. Because cropping equal proportions from each size class is not always the optimal way to thin a selection forest, management becomes rather complicated. For this reason, mathematical optimization has been used for finding the best structure, cutting cycle and harvest proportion for selection forests or other populations described by the transition-matrix model (Doubleday, 1975; Buongiorno and Michie, 1980).

In the present study the transition probabilities are based on an empirical single-tree growth model (Nyyssönen and Mielikäinen, 1978). The simulations made now could have been carried out by using the single-tree growth model directly. However, the matrix model has some advantages beyond empirical single-tree growth models. The model is simple and the simulations are fast and cheap. All the subprocesses of stand dynamics — i.e. birth, growth of
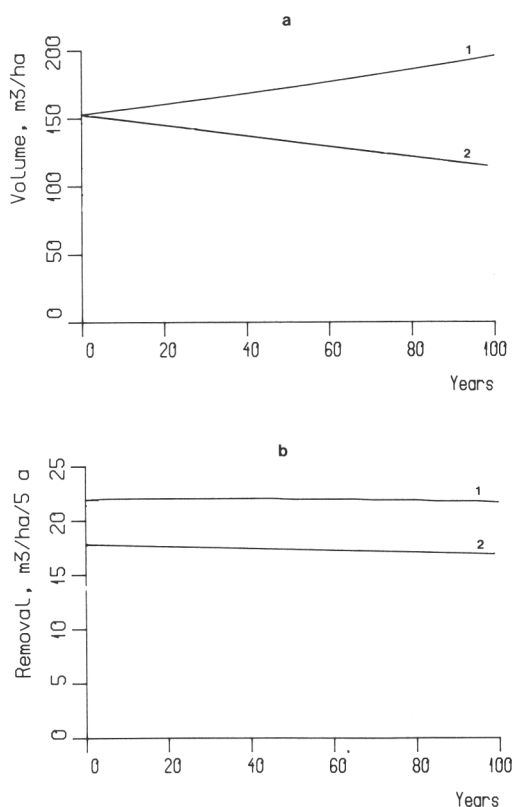
Fig. 7. Development of stand volume (a) and removal (b) when the real diameter growth is 20% greater (curve 1) or smaller (curve 2) than assumed in the model, and the cropping is equal to the sustained harvest proportion which is recalculated after every 5-year period by an erroneous model.

tree dimensions and mortality — can be incorporated into the same model. In addition, the matrix model itself holds some information about the dynamics of the stand in that it indicates the stable size-class distribution and the sustained-harvest proportion of the stand.

When constructing transition matrices for practical use, the greatest concern should be for those parameters that most affect the simulation results. In the present model the growth parameters (b-elements of the matrix) affect the simulation result linearly. For example, if the value of all b-elements is increased by 20% the sustained-harvest percentage and the volume of removal will also increase by 20%. If the value of all ingrowth parameters (c-elements in Equation 3) is doubled, the sustained-harvest proportion of stand whose basal area is 19.3 m^2 ha^{-1} would increase from 6.09% to 8.58%. If the value of c-elements is decreased by 50%, the sustained-harvest proportion would de-

crease to 3.85%. If the real growth of a stand deviates from the predicted growth and the stand is thinned according to sustained-harvest percentage computed by an erroneous model, the changes in the stand volume and removal are surprisingly small (Fig. 7). In general, the selection forest appears to be rather insensitive to small changes in thinning practice and the simulation model insensitive to small errors in parameters values.

The single-tree growth model (Nyyssönen and Mielikäinen, 1978) used for estimating the dependence of transition probabilities on stand structure is probably rather unreliable for predicting tree growth in a selection forest. Therefore, before using the program presented here in practical forest management, the growth and ingrowth parameters should be recalculated based on empirical measurements made in real selection forests. The transition probabilities can easily be determined by measuring the tree diameters at two timepoints in a number of uneven-aged stands. The ingrowth data should contain measurements on the number, age and height of trees shorter than 1.3 m. Using these data, more realistic models for transition probabilities and ingrowth could be developed.

There is a widely acknowledged need for information on selection management. Unfortunately there are presently no uneven-aged stands in Finland. The present study should therefore be taken as a preliminary attempt to throw light on the questions connected with managing uneven-aged spruce stands in Finland. According to this study, the annual production of a selection forest is around 5 m^3 ha^{-1} on a rather fertile site (*Oxalis-Myrtillus* type). This is clearly less than the maximum mean annual increment of 7.8 m^3 ha^{-1} for an even-aged spruce stand treated with thinnings (Koivisto, 1954), a result found earlier e.g. by Sarvas (1948). Some studies show, in addition, that growing Norway spruce stand over a very long time-span can cause a deterioration in the productivity and regeneration capability of the site (Sirén, 1955). Thus the growing of uneven-aged spruce stands in Finland cannot be justified by economics, although other objectives, for example soil protection or landscape management, may benefit.

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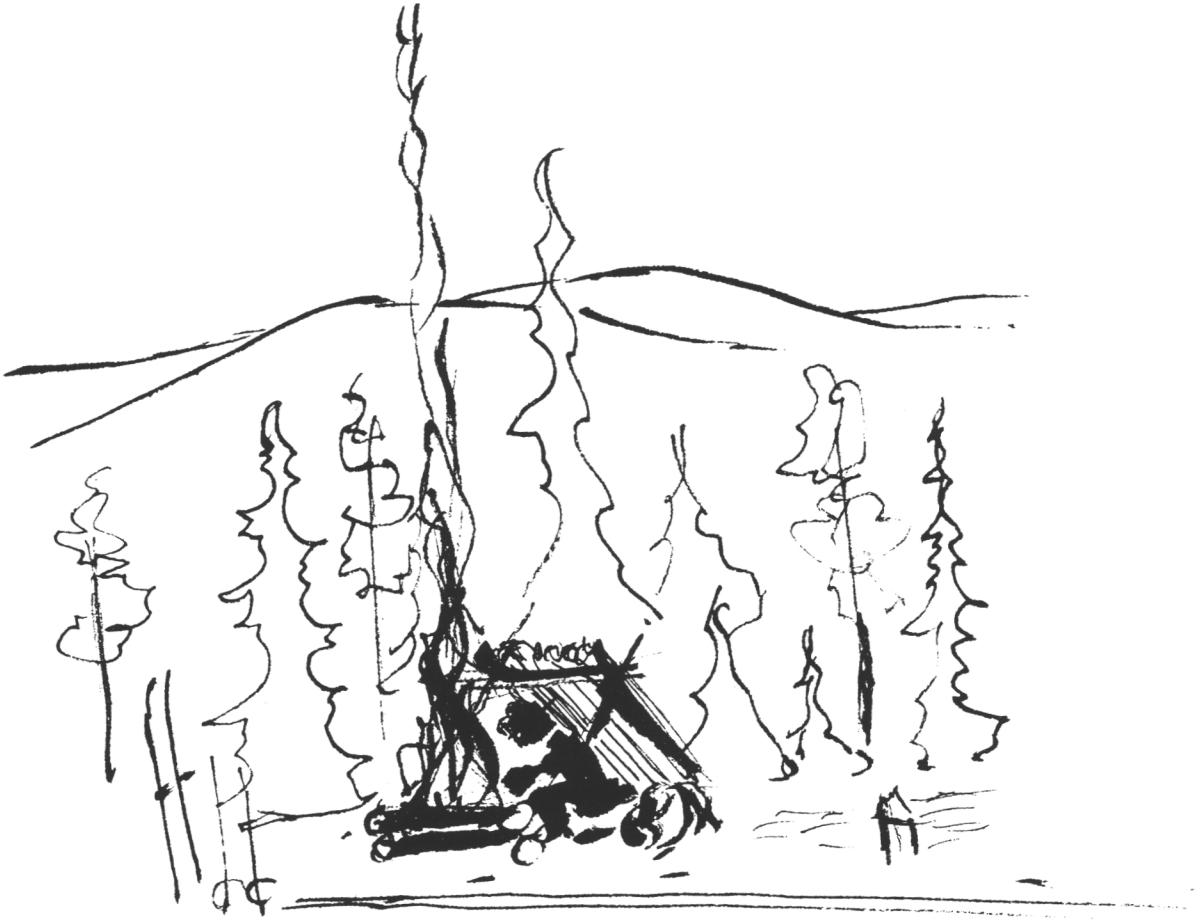
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III

Effect of spatial pattern of trees on the growth of a Norway spruce stand. A simulation model

Timo Pukkala & Taneli Kolström

TIIVISTELMÄ: TILAJÄRJESTYKSEN VAIKUTUS KUUSIKON KASVUUN. SIMULOINTIMALLI

Pukkala, T. & Kolström, T. 1991. Effect of spatial pattern of trees on the growth of a Norway spruce stand. Tiivistelmä: tilajärjestyksen vaikutus kuusikon kasvuun. Simulointimalli. Silva Fennica 25(3): 117–131.

The simulation model consists of a method to generate theoretical Norway spruce (*Picea abies* (L.) Karst.) stands, and a spatial growth model to predict the growth of these stands. The stand generation procedure first predicts the tree diameters from a few stands characteristics and from tree locations. Tree age and height are predicted using spatial models. Spatial growth models were made for both diameter growth and basal area growth. Past growth was used as a predictor in one pair of models and omitted in another pair. The stand generation method and the growth models were utilized in studying the effect of tree arrangement and thinning method on the growth of Norway spruce stand.

Simulointimalli koostuu menetelmästä, joka tuottaa teoreettisia kuusikoita (*Picea abies* (L.) Karst.), ja spatiaalisesta kasvumallista, jolla näiden mallimetsiköiden kasvu ennustetaan. Metsikköä generoitaessa ennustetaan ensin puun läpimitta metsikkötunnusten ja puiden koordinaattien avulla. Puun ikä ja pituus lasketaan spatiaalisilla malleilla. Tutkimuksessa esitetään spatiaalisia kasvumalleja läpimitan ja pohjapinta-alan kasvulle. Yhdessä malliparissa menneen kauden kasvu on yksi selittäjä, toisessa mennyttä kasvua ei ole käytetty. Mallimetsiköiden generointimenetelmää ja spatiaalisia kasvumalleja käyttäen selvitettiin puiden tilajärjestyksen, ajourien ja harvennustavan vaikutusta kuusikon kasvuun.

Keywords: spatial distribution, simulation models, growth, biological competition, *Picea abies*.
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Symbols

Stand characteristics

A	Hopkins' grouping index
$D_{<5}$	Unweighted mean diameter of trees within a 5-m circle around the subject tree, subject tree included, cm
D_g	Mean diameter, weighted by basal area, cm
$D_{<5(g)}$	Mean diameter (weighted by basal area) of trees within 5 m from the subject tree, subject tree included, cm
D_{max}	Maximum diameter, cm
D_{min}	Minimum diameter, cm
G	Stand basal area, m²/ha
$G_{<5}$	Basal area of neighbors nearer than 5 m, subject tree excluded, m²/ha
$G_{<5>d}$	Basal area of neighbors nearer than 5 m and greater than the subject tree, m²/ha
H_g	Mean height, weighted by basal area, cm
H_{dom}	Dominant height, m
N	Number of trees per hectare
$N_{<5}$	Number of trees per hectare within a 5-m circle around the subject tree (subject tree included)
R	Grouping index of Clark and Evans
$S_{<5}$	Mean distance of neighbors nearer than 5 m, m; if there are no neighbors $S_{<5} = 6$
s_d^2	Variance of diameter within the circle, cm²
T	Age at breast height, weighted by basal area, years
$\sum d_j/s_j$	Sum of ratios of diameter and distance of neighbors nearer than 5 m, subject tree excluded, cm/m
$\sum d_j/s_j(q3)$	Sum of ratios of diameter and distance of neighbors nearer than 5 m, the neighbors are selected with relascope using basal area factor 3 m²/ha, cm/m
$\sum d_j/s_j(q2)$	Sum of ratios of diameter and distance of neighbors nearer than 5 m, the neighbors are selected with relascope using basal area factor 2 m²/ha, cm/m

Tree characteristics

d	Diameter at breast height, cm
g	Basal area, cm²
h	Height, m
i_d	Future 5-year diameter growth including bark, cm
i_{d-5}	Past overbark 5-year diameter growth, cm
i_g	Future 5-year basal area growth including bark, cm²
i_{g-5}	Past overbark 5-year basal area growth, cm²
t	Age at breast height, a

Others

R^2	Degree of determination
$s_e\%$	Relative standard error of estimate, $100\sqrt{(\exp(s_f^2/2)-1)}$
s_f	Standard deviation of the dependent variable around the function

Timo Pukkala & Taneli Kolström

1 Introduction

The results of empirical studies are most conveniently expressed as mathematical models which allow a free and detailed exploration of the relationships found in the investigation. When studying the effect of spatial pattern of trees on stand productivity the target model is a distance dependent single tree growth model. It enables the prediction of stand growth with different tree arrangements.

If one wishes to analyze theoretical stands and situations, there is also a need for a method to produce the theoretical stands. Even though these stands are theoretical, they should be sensible and conceivable. This means that the relationships between stand and tree characteristics in the model stands should be similar to that which natural birth, growth and death processes can produce. Otherwise the results of simulations cannot be generalized to practical situations.

The methodology to theoretically examine the effect of spatial pattern on stand productivity has recently been developed for Scots pine (Pukkala 1989a, 1989b). In the first step of this method, the tree dimensions are generated from tree locations and some stand characteristics. The growths of the resulting trees are predicted in the second step using a spatial growth model.

This study aimed at developing the corresponding models for Norway spruce (*Picea abies* (L.) Karst.) stands. The models prepared were used to analyze the effect of spatial pattern and thinning method on the stand growth.

2 Methods

2.1 Generation of model stands

Definition of a model stand

For yield investigation purposes the stand is defined accurately enough if the following characteristics are known for each tree: location, species, age, diameter at breast height and height. The age is usually required as the breast height age since growth models commonly use this predictor.

When studying the effect of spatial distribution of trees on stand productivity it is hoped that everything but the spatial pattern is similar in the stands which are to be compared, i.e. stands have exactly the same age, diameter distribution, dominant height and stand volume. However, this is usually unrealistic since spatial pattern affects the development of stand characteristics and their relations. Only immediately after systematic thinnings (e.g. row harvesting) can the diameter distribution and stand characteristics be similar in different tree arrangements.

When it is not logical to have all the stand parameters except tree locations similar in all model stands, the stands should at least have the same growing site, age and density. Otherwise it is not easy to distinguish the effect of spatial distribution from the effects of other factors.

In older stands, stand density is usually expressed as basal area. Site fertility can be defined as the relationship between age and dominant height. This relationship is not greatly affected by stand density, spatial pattern of trees and usual thinnings.

Therefore, if a simulation compares stands with the same forest site type, age and density, it can be assumed that the following stand characteristics are known when the generation of a model stand starts: tree species, stand age, dominant height and basal area or number of trees per hectare.

Steps in the generation of model stands

The adopted method of producing Norway spruce model stands is divided into the following steps:

(1) Decide the stand age (T), dominant height (H_{dom}) and stand basal area (G). Obtain a sensible number of trees per hectare (N) either as a model prediction or from other sources.
(2) Generate the coordinates of trees as a realization of a suitable spatial process.
(3) Calculate the tree diameters (d) from T, H_{dom}, G, N and tree locations.
(4) Calculate the breast height age (t) of each tree from d, T, H_{dom}, G, N and tree locations.
(5) Calculate tree heights (h) from d, t, T, H_{dom}, G, N and tree locations.

The prediction models for tree characteristics (d, t, and h) make a recursive set of equations where model predictions appear as predictors in the subsequent models. This does not improve the predictions from what can be obtained with the help of T, H_{dom}, G, N and tree locations only, but it assures that diameter, height and age are logically related to each other. In the absence of a proper growth model, this height model facilitates the simulation of height development better than a model which omits the tree age.

Models used to generate tree dimensions explain only part of the variation in tree dimensions. Therefore, to get the tree dimensions to vary in model stands as much as the variation in real stands, residual variation must be added as a stochastic component to the model prediction. In this study, stochastic component was added to the diameter and age models. The height model was used in simulations for incrementing the tree height, and a normally distributed stochastic term could have created negative growths.

Even though the model stands generated by the system may have the same input values for T, H_{dom}, G and N, their realized values are seldom exactly the same. This is because of the stochasticity of the method.

Prediction of tree diameter

Two different approaches were used to predict tree diameter as a function of T, H_{dom}, G, N and tree locations (Pukkala 1989a). In the first method (referred to as Method 1), diameter was predicted directly from stand characteristics and the number and distance of close neighbors. A stochastic term corresponding to the residual variation was added to the prediction.

The second method (Method 2) first predicted the local diameter distribution and then randomly took one diameter from it. Local diameter distribution was calculated for each tree from a circular area, the subject tree located in the center. The beta distribution was used as the theoretical local distribution. It can be calculated from the minimum, mean, maximum and variance of diameter. These variables were predicted from stand characteristics (T, H_{dom}, G and N) and the number of trees in the circle.

2.2 Spatial growth model

Common predictors of empirical diameter growth models are: site fertility, present diameter, age of the tree, relative size of the tree, stand density or competition, sometimes also past growth and removal (e.g. Eriksson 1976, Pukkala 1989b, Tham 1989). Relative size can be expressed as the ratio of tree diameter and the mean diameter of the stand. Stand density or competition may be described as the stand basal area. Site fertility index may be a separate predictor or its effect can be expressed through stand age and other characteristics.

In a spatial model part of the predictors, such as relative size and stand density, are computed separately for each tree from the locations and dimensions of close neighbors. Local stand density is usually expressed with a competition index which takes into account the size, proximity and number of competing neighbors.

Trees which are taken into account when calculating competition indices can be selected with different criteria. The simplest way is to take all trees nearer than a certain limit into the index. Another possibility is to use a relascope so that bigger trees are included from longer distances than small individuals. It is also possible to take into account the size difference between the subject tree and the neighbor e.g. by computing the index separately for bigger neighbors and smaller neighbors (Tham 1989). All these approaches were also utilized in the present study when searching for predictors of distance dependent growth models and other spatial tree models.

All the ways to calculate competition index need a limiting distance beyond which trees are no longer considered as competitors. Because competition indices are usually computed in such a way that the contribution of a tree to the index sharply decreases with distance, the indices or the growth models are not particularly sensitive to changes in the limiting distance. The distance

affects more the measurement and the use of the study material. The limit defines the width of the border zone which is needed when measuring empirical sample plot material or selecting observations: the shorter the limit, the nearer the plot edge the observation can be situated and the bigger the number of trees that can be used for constructing the models.

In this study the effect of limiting distance was examined by calculating different growth models where the limiting distance was 4 m, 5 m or 6 m. The residual variation usually decreased with increasing limiting distance but the difference between 5 m and 6 m was negligible. Therefore, 5 m was selected as the competition distance of this study. This limiting distance was also used in models for tree dimensions.

3 Material

3.1 Measurements

The models were computed from 16 plots measured in pure Norway spruce stands in North Karelia. Another set of 7 plots were used for testing the models. The plot size varied according to the number of stems per hectare; the number of trees further than five meters from the nearest plot edge was 40–80 in each plot. The stand age, density and spatial distribution of trees varied considerably (Table 1). The site fertility was either good (*Oxalis-Myrtillus* type) or medium (*Myrtillus* type). Part of the plots were situated in naturally regenerated stands

Table 1. Stand characteristics of the study plots. Parameters R and A are the grouping indices of Clark and Evans, and Hopkins, respectively.

Plot	N	G	T	H_{dom}	D_g	H_g	R	A
Study plots								
1	1592	41.0	42.7	22.2	23.5	18.0	1.19	0.80
2	767	35.0	37.4	21.5	25.6	19.6	1.26	0.67
3	778	22.0	34.9	20.2	21.6	18.2	1.30	0.69
4	733	27.1	36.3	20.5	23.1	18.8	1.29	0.60
5	830	8.6	16.5	9.9	18.9	9.1	1.11	1.33
6	883	19.3	29.3	17.8	22.8	15.4	1.12	1.26
7	647	22.7	70.6	24.6	26.5	21.0	1.18	0.87
8	208	20.5	70.5	24.7	39.4	24.1	1.25	0.70
9	587	22.7	41.2	20.6	23.4	18.8	1.35	0.46
10	448	22.5	38.9	21.8	27.8	20.5	1.21	0.68
11	208	18.4	77.8	24.9	37.2	24.3	1.26	0.75
12	1053	30.0	40.1	20.3	21.6	18.0	1.17	1.48
13	506	27.5	38.1	21.2	28.0	19.7	1.17	0.88
14	660	22.7	42.0	19.7	22.0	18.5	1.32	0.52
15	840	12.5	15.4	11.5	15.3	10.3	1.08	2.56
16	258	13.1	66.1	21.5	35.8	20.8	1.22	0.60
Test plots								
1	517	30.1	54.0	25.8	36.9	23.2	0.93	1.23
2	1130	30.5	77.4	25.5	34.5	22.0	0.86	1.41
3	1317	30.7	59.6	19.6	22.8	16.8	1.00	0.81
4	760	15.2	35.5	17.5	21.8	15.8	0.91	1.01
5	1300	27.8	59.5	24.3	27.7	20.2	1.16	0.63
6	1967	28.5	44.8	19.4	22.7	15.6	0.93	0.78
7	1767	16.1	64.3	16.3	15.4	12.2	0.83	2.39

and another part in plantations. The stands had been managed normally. The time since previous thinning was always at least five years.

The diameter and coordinates were measured for each tree and stump. Trees further than five meters from the plot edge were measured also by height, age and the annual radial growths of the past 10 years. However, if the tree top was difficult to see, the height was not measured but predicted with the help of diameter using a model which was based on the measured heights and diameters. Age and growth were measured from a core taken at breast height. If the core was unclear, the growth measurements were omitted and the age was predicted from diameter. The bark thickness was measured from 20 trees per plot.

The total number of trees further than five meters from the nearest plot edge was 944. The breast height age was measured for 861 trees, height for 822 trees and radial growth for 860 trees.

3.2 Computations

In the first step of the computations of a plot the measurements were used for models that predicted the tree height, age, bark thickness or radial growth as a function of diameter. The model was always a linear model ($y = a + bx$) except the height model which was the Näslund's (1936) height curve ($y = 1.3 + x^2/(a + bx)^2$). These models were utilized if a measurement was missing.

The measured or estimated tree dimensions were used for computing the following stand characteristics: age, dominant height, basal area and number of stems per hectare. Additional predictors for models that predicted tree dimensions (diameter, age and height) were computed in the second step. In the diameter model, when Method 1 was used (see above), the predictors described the number and proximity of neighbors (see Pukkala 1989a). With Method 2 the

Table 2. Range and mean of some characteristics within 860 trees which were used for constructing spatial growth models.

Variable	Minimum	Maximum	Mean	Unit
i_d	0.0500	7.470	1.515	cm/5 a
i_g	0.8000	243.8	42.11	cm²/5 a
d	0.3400	55.42	18.75	cm
t	3.0000	93.00	34.44	a
h	1.3700	29.31	15.79	m
$G_{<5}$	0.0000	54.46	20.05	m²/ha
$\sum d_j/s_j$	0.0000	137.6	33.85	cm/m

number of trees and the minimum, mean, maximum and variance of diameter were computed for each tree from a circular area around the tree.

Several predictors were computed for the age and height models from tree locations and diameters. They described the amount of competition that the tree faces and were similar to the competition indices of spatial growth models. Only those trees for which the age or height was measured were used for constructing the model. The rest of the trees were used for computing predictors.

The future five-year overbark growth was selected as the predicted variable of the spatial growth model. In order to predict future growth, tree dimensions five years earlier were derived. Double bark thickness and 5-year diameter growth (without bark) were subtracted from the present diameter. Overbark diameter and overbark diameter growth were computed assuming that the proportion of bark had been the same for the past five years. The future five-year diameter growth 10 years ago (past five-year growth 5 years ago) was computed similarly.

The tree dimensions five years ago were used for calculating stand characteristics, different competition indices and other potential predictors of the spatial growth model (Table 2).

4 Results

4.1 The method for generating model stands

Models

In the present study material the number of stems per hectare was dependent on stand age, dominant height and basal area as follows:

	Coefficient	Predictor	t-value
$\ln(N) =$	8.409		36.0
	−0.01674	× T	5.3
	+1.368	× $\ln(T)$	7.4
	−3.885	× $\ln(H_{dom})$	20.8
	+1.729	× $\ln(G)$	38.6 (1)

$$R^2 = 0.780 \quad s_f = 0.245 \quad s_e\% = 17.5$$

The number of stems per hectare of the model stands to be generated by the system should be close to the prediction of Equation (1). Otherwise the predicted tree dimensions may be unreliable or biased.

With Method 1 the tree diameter is predicted directly from stand characteristics and the number and vicinity of neighbor trees:

	Coefficient	Predictor	t-value
$d^{0.5} =$	7.995		7.4
	+0.2369	× $S < 5$	5.2
	−0.3911	× $\ln(N_{<5})$	5.7
	−0.06986	× G	4.9
	+3.342	× $\ln(G)$	9.0
	−1.376	× $\ln(H_{dom})$	4.9
	−0.9925	× $\ln(N)$	7.9 (2)

$$R^2 = 0.460 \quad s_f = 0.730$$

where $S_{<5}$ = mean distance of neighbors nearer than 5 m (m) if there are no neighbors $S_{<5=6}$
$N_{<5}$ = number of trees per hectare within 5 m (subject tree included)

The model explains 46 % of the variation in tree diameter. In simulations, the residual variation should be generated by adding to the predicted $d^{0.5}$ a normally distributed stochastic term which has a zero mean and a standard deviation equal to 0.730.

When using Method 2 for generating tree diameters the following set of models are needed to calculate the local diameter distribution:

	Coefficient	Predictor	t-value
$\ln(D_{<5}) =$	4.162		19.4
	−0.1443	× $\ln(T)$	6.5
	−0.02475	× G	8.2
	+1.230	× $\ln(G)$	19.2
	−0.4496	× $\ln(N)$	17.2
	−0.1479	× $\ln(N_{<5})$	9.7 (3)

$$R^2 = 0.773 \quad s_f = 0.162 \quad s_e\% = 11.5$$

	Coefficient	Predictor	t-value
$\ln(D_{min}) =$	20.62		21.3
	−0.1272	× T	18.9
	+6.564	× $\ln(T)$	19.7
	+1.035	× H_{dom}	20.6
	−23.06	× $\ln(H_{dom})$	23.3
	−0.153	× G	18.4
	+4.639	× $\ln(G)$	19.0
	−0.3577	× $\ln(N)$	7.0
	−0.1815	× $\ln(N_{<5})$	6.9
	+1.292	× $\ln(D_{<5})$	24.3 (4)

$$R^2 = 0.822 \quad s_f = 0.261 \quad s_e\% = 18.6$$

	Coefficient	Predictor	t-value
$\ln(D_{max}) =$	−22.41		24.3
	+0.128	× T	23.5
	−6.038	× $\ln(T)$	23.6
	−1.074	× H_{dom}	26.1
	+22.55	× $\ln(H_{dom})$	27.2
	+0.2122	× G	23.6
	−5.24	× $\ln(G)$	23.6
	−0.001406	× N	14.8
	+1.145	× $\ln(N)$	16.3
	+0.1065	× $\ln(N_{<5})$	7.9
	+0.04652	× $D_{<5}$	34.1 (5)

$$R^2 = 0.828 \quad s_f = 0.134 \quad s_e\% = 9.5$$

	Coefficient	Predictor	t-value
$\ln(s_d^2) =$	3.491		26.3
	−0.00008286	× N	6.3
	+0.0003596	× $N_{<5}$	15.4
	−0.6721	× $\ln(N_{<5})$	31.7
	+0.9987	× $\ln(D_{max}−D_{min})$	574.9 (6)

$$R^2 = 0.999 \quad s_f = 0.094 \quad s_e\% = 6.7$$

where $D_{<5}$ = unweighted mean diameter of trees within a 5-m circle around the subject tree, subject tree included (cm)
D_{min} = minimum diameter within the circle (cm)

D_{max} = maximum diameter within the circle (cm)
s_d^2 = variance of diameter within the circle (cm^2)

The beta distribution is computed from $D_{<5}$, D_{min}, D_{max} and s_d^2 (Loetsch et al. 1973, p. 53). This distribution is sampled to obtain a diameter for the subject tree. Equations (3)–(6) again constitute a recursive chain of models. This means that the predictions for D_{min}, D_{max} and s_d^2 are not as good as the presented R^2, s_f and $s_e\%$ suggest. The use of estimated $D_{<5}$ for predicting D_{min}, D_{max} and s_d^2 assures that these parameters are logically related to each other. Another way to take into account correlations between D_n, D_{min}, D_{max} and s_d^2 is to compute covariances of residuals of models for D_n, D_{min}, D_{max} and s_d^2, these models being based on known predictors only. When using the models, four stochastic components are sampled from the joint distribution of the residuals.

The spatial models for predicting tree age and height complete the method for generating model stands:

	Coefficient		Predictor	t-value
$\ln(t) =$	−0.2733			4.6
	+0.1208	×	$d^{0.5}$	10.2
	+0.006497	×	$G_{<5>d}$	10.2
	+0.2859	×	$d/D_{<5(g)}$	9.8
	+0.8883	×	$\ln(T)$	43.7 (7)

$$R^2 = 0.847 \quad s_f = 0.181 \quad s_e\% = 12.9$$

	Coefficient		Predictor	t-value
$\ln(h\text{-}1.3) =$	3.667			205.7
	−19.72	×	$1/(d+5)$	51.3
	−7.732	×	$1/(t+5)$	14.3
	+0.002599	×	$G_{<5}$	5.4 (8)

$$R^2 = 0.901 \quad s_f = 0.150 \quad s_e\% = 10.6$$

where $G_{<5>d}$ = basal area of neighbors nearer than 5 m and greater than the subject tree (m^2/ha)
$D_{<5(g)}$ = mean diameter (weighted by basal area) of trees within 5 m from the subject tree, subject tree included (cm)
$G_{<5}$ = basal area of neighbors nearer than 5 m, subject tree excluded (m^2/ha)

The models for tree diameter indicate that an increase in the number of trees within a subarea of a stand shifts the diameter distribution to-

wards smaller diameters. A tree which faces much competition is older and taller than a tree with the same diameter and less competition.

Validity of the models

The validity of the stand generation method was tested by computing the diameter, breast height age and height of each tree in the 7 test plots with Equations (2)...(8) and comparing the stand characteristics computed from these predictions to those computed from the measurements. The residual variation of the models was simulated with normally distributed random numbers.

Both the basal areas and the mean heights computed from the predictions frequently differ from the measured values (Fig. 1). This is partly
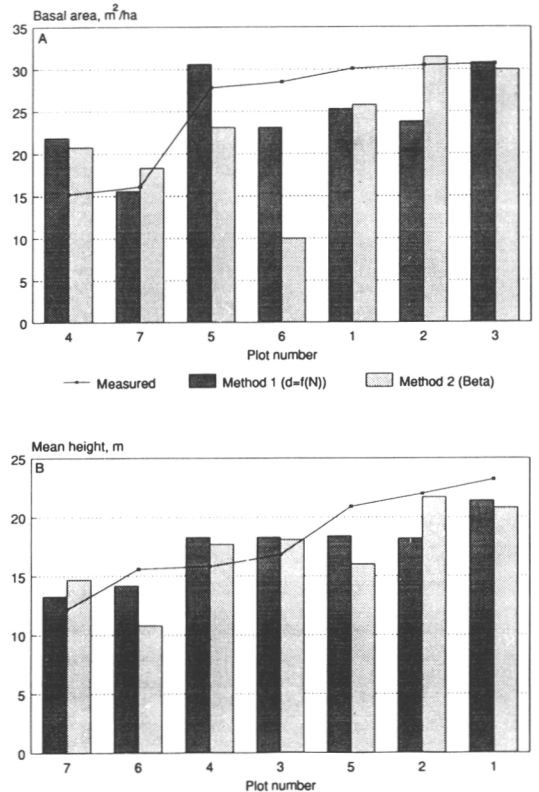

Fig. 1. Measured and predicted stand basal area (A) and mean height (B) of the seven test plots. Predicted stand characteristics are based on tree dimensions calculated from stand basal area, number of stems per hectare, age, dominant height and tree locations.

due to the stochasticity of the stand generation method and partly due to inadequacies of the models. The differences between measured and predicted stand dimensions are greatest in test plot 6 where both methods produced too small

Fig. 2. Crown maps of study plots 1, 5, 9 and 13. Crown width (dc, m) is calculated by equation dc = 0.5 + 0.1 × d, where d is breast height diameter (cm). The small dots represent stumps.

trees, especially Method 2. Test plot 6 has more stems per hectare than any of the study plots used to compute the models. It seems that, outside the range of variation in the study material, the models for diameter and diameter distribution over estimate the effect of number of stems.

Plots 1, 5, 9 and 13 were used for a more thorough analysis of the diameter models (Fig. 2). Both methods to generate tree diameters produced distributions more or less similar to the measured ones (Fig. 3). In plot 9 both methods produced too many small diameters (9–15 cm), and in plot 5 the distribution generated by Method 2 was too narrow.

The methods were tested at tree level by computing correlation coefficients between diameter and variables describing the number and proximity of neighbors; the coefficients should be similar in real and generated stands (Table 3). The results indicate that in this respect Method 1 (direct prediction of diameter) is better than Method 2 (estimation of local diameter distribution). Because Method 2 is was not bet-
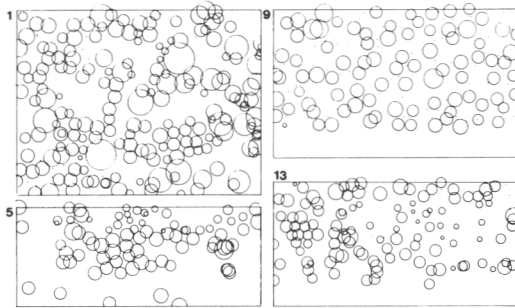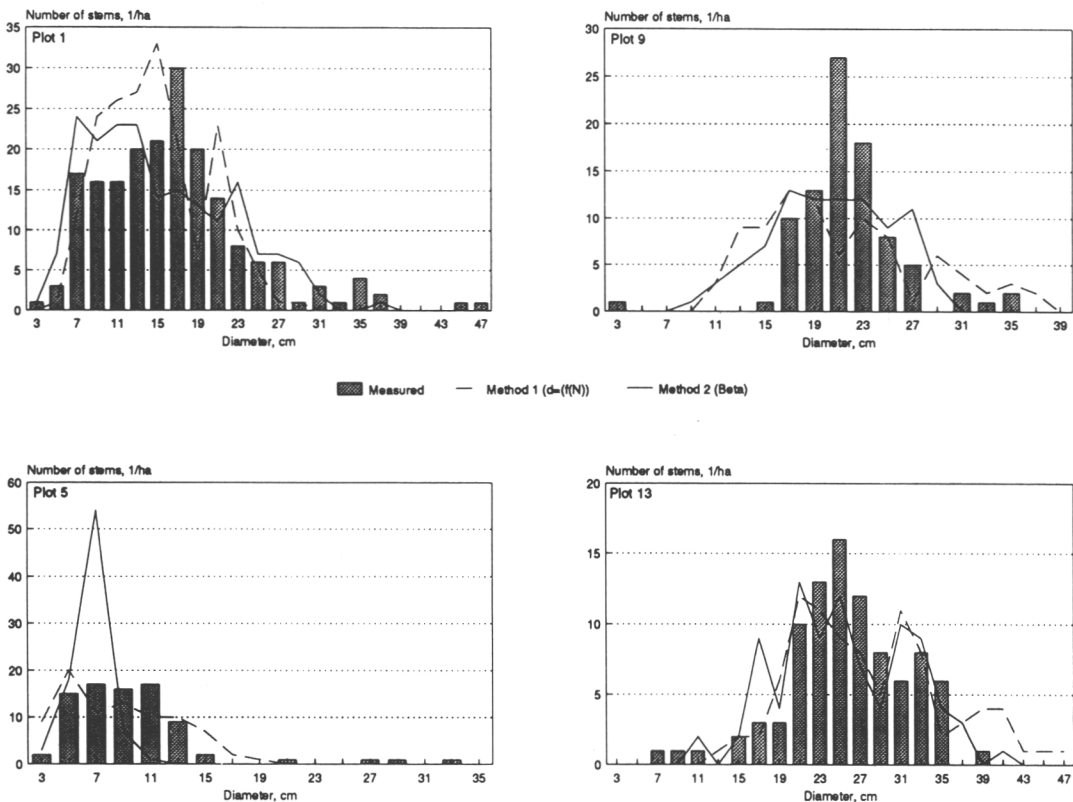

Fig. 3. Measured and predicted diameter distribution of study plots 1, 5, 9 and 13. Diameters were predicted with Equation (2) (Method 1) or Equations (3)–(6) (Method 2).

Table 3. Correlation coefficient between tree diameter and some variables describing the number and proximity of neighbor trees. $S_{<5}$ is the mean distance of neighbors nearer than 5 m. $\Sigma 1/s_j$ is the sum of inverted distances of these neighbors. In Method 1 the diameter is predicted from the number and locations of neighbors and in Method 2 is the sample from the predicted local diameter distribution.

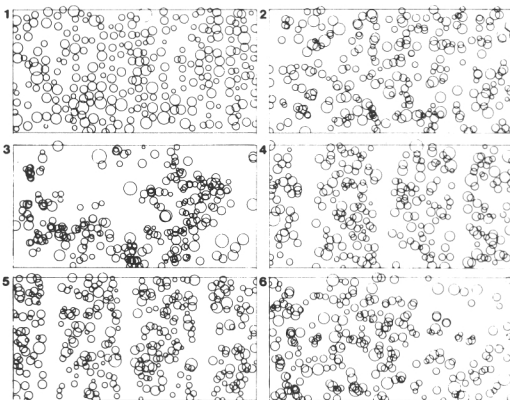| Plot	Measured	Method 1	Method 2	Measured	Method 1	Method 2
	Correlation with $S_{<5}$			Correlation with $\Sigma 1/s_j$		
1	0.273	0.065	0.083	−0.180	−0.110	0.001
5	0.242	−0.148	−0.092	−0.170	−0.316	0.016
9	0.016	0.127	−0.122	−0.193	−0.024	−0.218
13	−0.074	0.342	0.174	−0.045	−0.429	−0.212
Mean	0.114	0.097	0.011	−0.147	−0.220	−0.103
1 + 5 + 9 + 13	0.333	0.404	−0.105	−0.506	−0.591	−0.162

Fig. 4. Examples of stands (crown maps) generated by Method 1. In stand 5 the extraction roads are new. In the other stands the spatial distribution has remained unchanged for several years. Stands 1, 2, 3, 4 and 6 were used in the simulation experiment of Section 5.1. The area of each plot is 40 m × 80 m.

ter than Method 1 at the stand level, Method 1 should be preferred in producing Norway spruce model stands. Method 1 has the additional advantage of being much simpler than Method 2.

The use of the above models for generating tree dimensions presupposes that the present spatial arrangement has affected the tree growth for a long time; the latest thinning has taken place at least five years ago. The procedure can

be combined with simulated thinnings to create such differences in the spatial distribution which have a recent origin.

Examples of model stands generated by Method 1 are given in Fig. 4. In stand 5 of Fig. 4 the extraction roads are new (created after the generation of diameters), and in stand 4 they have an older origin.

4.2 Spatial growth models

Spatial growth models were computed for a five-year basal area growth (i_g) and diameter growth (i_d). One pair of models was made by using past growth as a predictor and another pair without past growth:

	Coefficient		Predictor	t-value
$\ln(i_g) =$	4.102			25.5
	+0.9323	×	$d^{0.5}$	16.4
	−0.0009224	×	g	7.5
	+1.231	×	$\ln(1/(t + 5))$	20.3
	−0.01452	×	$\Sigma d_j/s_j$	15.4
	+1.037	×	$d/D_{<5(g)}$	9.5 (9)

$R^2 = 0.738$ $s_f = 0.490$ $s_e\% = 35.7$

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Coefficient		Predictor	t-value
$\ln(i_g) =$	0.5679		7.1
	−0.005786	× $i_{g\text{-}5}$	9.5
	+1.196	× $\ln(i_{d\text{-}5})$	40.3
	+0.7016	× $d^{0.5}$	23.1
	−0.0004445	× g	6.1
	−0.006379	× $\sum d_j/s_j$	11.2
	+0.2683	× $d/D < 5(g)$	3.9 (10)

$$R^2 = 0.905 \quad s_f = 0.296 \quad s_e\% = 21.2$$

Coefficient		Predictor	t-value
$\ln(i_d) =$	4.336		19.8
	+0.04982	× h	7.8
	+1.372	× $\ln(1/(t + 10))$	19.6
	−0.01506	× $\sum d_j/s_j(q3)$	16.5
	+0.9481	× $d/D_{<\,5(g)}$	10.6 (11)

$$R^2 = 0.595 \quad s_f = 0.472 \quad s_e\% = 34.3$$

Coefficient		Predictor	t-value
$\ln(i_d) =$	−0.1335		2.1
	−0.1650	× $i_{d\text{-}5}$	8.0
	+1.176	× $\ln(i_{d\text{-}5})$	29.5
	+6.357	× $1/(t + 10)$	5.0
	−0.006213	× $\sum d_j/s_j(q2)$	11.1
	+0.3047	× $d/D_{<\,5(g)}$	5.9 (12)

$$R^2 = 0.850 \quad s_f = 0.287 \quad s_e\% = 20.5$$

where i_g = future 5-year basal area growth including bark (cm²)
g = basal area of tree (cm²)
$\sum d_j/s_j$ = sum of ratios of diameter (cm) and distance (m) of neighbors nearer than 5 m, subject tree excluded (cm/m)
$D_{<\,5(g)}$ = mean diameter (weighted by basal area) of trees within 5 m of the subject tree, subject tree included (cm)
$i_{g\text{-}5}$ = past overbark 5-year basal area growth (cm²)
$i_{d\text{-}5}$ = past overbark 5-year diameter growth (cm)
i_d = future 5-year diameter growth (cm)
h = tree height (m)
$\sum d_j/s_j(q3)$ = sum of ratios of diameter (cm) and distance (m) of neighbors nearer than 5 m, the neighbors are selected with a relascope using basal area factor 3 m²/ha (cm/m)
$\sum d_j/s_j(q2)$ = sum of ratios of diameter (cm) and distance (m) of neighbors nearer than 5 m, the neighbors are selected with a relascope using basal area factor 2 m²/ha (cm/m)

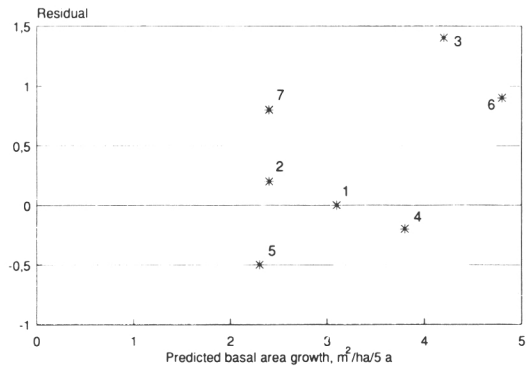Fig. 5. Error in the predicted basal area growth (m²ha⁻¹a⁻¹) of the test plots 1–7 as a function of prediction. Predicted growth is calculated by Equation (9).

Using past growth as an additional predictor improved the models considerably. However, spatial predictors were still needed. This indicates that there are temporal changes in the competitive status of a tree. These changes may belong to a normal stand development or they may have been created through thinnings.

When the aim is to predict the volume growth of a stand as accurately as possible, it is preferable to predict basal area growth instead of diameter growth. In practical situations the past growth is seldom available for growth prediction. Equation (9) can therefore be considered as the most important growth model of the study.

Equation (9) was tested by predicting the future 5-year growth (five years ago) of each tree in the 7 test plots. The basal area growth of the plot was computed both from the predicted and measured diameter growths (Fig. 5). The predictions were near the measured growths in plots 1, 2, 4 and 5, but in plots 3, 6 and 7 underestimation was notable. These plots have a rather high number of stems per hectare and the trees are quite small (Table 1). This indicates that Equation (9) overestimates the effect of competition in dense stands consisting of small trees. In plot 7 an additional reason might be the high degree of aggregation of trees (Table 1) the effect of which may not be fully reflected in the growth model.

5 Simulation experiments

5.1 Effect of spatial pattern of trees on stand growth

The first simulation experiment examined the effect of such differences in the spatial distribution of trees that had existed for a long time. Stands 1, 2, 3, 4 and 6 of Fig. 4 were used in the comparison. The trees were generated from the following stand characteristics: basal area (G) 25 m²/ha, breast height age (T) 40 years, dominant height (H_{dom}) 20 m and number of stems (N) 848 trees/ha (prediction of Equation 1). The tree coordinates were generated as follows.

(1) Systematic grid but with some mortality and random deviations from the grid points (a tree plantation).
(2) Poisson distribution.
(3) Trees are in clusters which are Poisson distributed. There are 15 trees in each cluster (average) and the radius of a cluster is 7 m.
(4) Five meters wide extraction roads 25 m apart in a non-stationary Poisson process with 1 m hard core. Number of stems per hectare decreases by 20 % from the middle of two roads to the road edge. The minimum distance (hard core) between any two trees is 1 m.
(6) Non-stationary Poisson distribution where the number of stems per hectare changes in a trend-like manner. The relative number density is 1 in the lower left hand corner and decreases linearly down to 0.25 in the upper right hand corner.

The grouping indices of Clark and Evans (1954) and Hopkins (1954) were used to describe the degree of clustering of the stands. The index of Clark and Evans (R) is

$$R = v^2 \sqrt{\mu} \qquad (13)$$

where v is the mean distance from a tree to the nearest neighbor and μ is the stand density (trees/m²). The index of Hopkins (A) is computed by the formula

$$A = \Sigma a_i^2 / \Sigma b_j^2 \qquad (14)$$

where a_i is a random 'point to nearest tree' distance and b_j is a random 'tree to nearest neighbor' distance. The number of both distances is the same. For Poisson distribution both indices
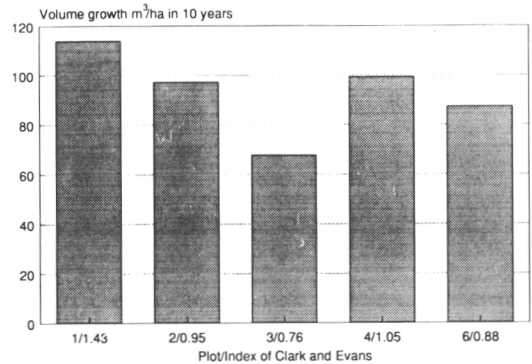

Fig. 6. Predicted growth of stands 1, 2, 3, 4 and 6 of Fig. 4.

have an expected value of one. For a regular patter R is greater than one and A less than one, and for aggregated distributions R is less than one and A greater than one.

For the model stands used in the simulation, indices R and A of these stands were as follows:

Stand	R	A
1	1.43	0.36
2	0.95	0.94
3	0.76	3.41
4	1.05	1.25
6	0.88	1.48

According to the indices, stand 1 is the most regular and stand 3 clearly the most clustered.

The growth of each stand was simulated for 10 years using Equation (9). The height corresponding to the incremented diameter was calculated using Equation (8) and the stem volume using the volume function of Laasasenaho (1982). It was supposed that the plots had similar plots on all sides.

The predicted growth of the model stands clearly decreased with clustering (Fig. 6). The growth of stand 3 was 40 % lower than in the most regular, stand 1. Five meter wide extraction roads decreased the growth by about 15 % when many trees had been cropped from the ride sides (stand 4). The correlation coefficient of growth prediction is 0.909 with grouping index R and –0.964 with index A.

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5.2 Effect of thinning method on stand growth

The second simulation studied the effect of thinning on stand productivity. Before the thinning treatment the stand basal area was 31.8 m²/ha, age 38.9 years, dominant height 20.6 m and number of trees per hectare 2063. The spatial distribution was similar to plot 3 in the previous simulation experiment (clustered). This stand was thinned to a remaining basal area of 22 m²/ha according to the following principles (Fig. 7):

(1) Removed trees were selected at random.
(2) 4.5 meter wide extraction roads were cleared at 30 meter distances. The rest of the removal (4 m²/ha) was taken at random.
(3) Trees were removed on the basis of diameter only, starting from the biggest tree (thinning from above).
(4) Trees were removed on the basis of diameter only, starting from the smallest tree (thinning from below).
(5) The smaller tree of each pair closer than 1 m was removed, after which rule (4) was applied.

After thinning the grouping indices R and A indicated a slightly regular distribution for thinning method 5 and clustered patterns for the other methods:

Stand	R	A
1	0.85	2.15
2	0.77	2.14
3	0.83	1.64
4	0.89	1.62
5	1.08	0.78

The best growth was obtained for rule 5, with a thinning regime which removed small trees and aimed, at the same time, for a regular spatial distribution (Fig. 8). The growth prediction was poorest for the method that removed the biggest trees without considering the spatial distribution (rule 3). Rule 5 closely resembles a practical execution of a thinning treatment. In this simulation experiment the correlation coefficient between the predicted growth and grouping index R was 0.877, and –0.741 between growth and index A.
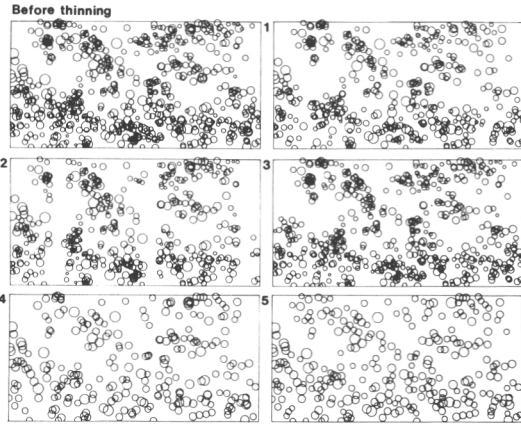

Fig. 7. Crown map of a model stand before thinning and after 5 different thinnings. The area of the plot is 40 m × 80 m.
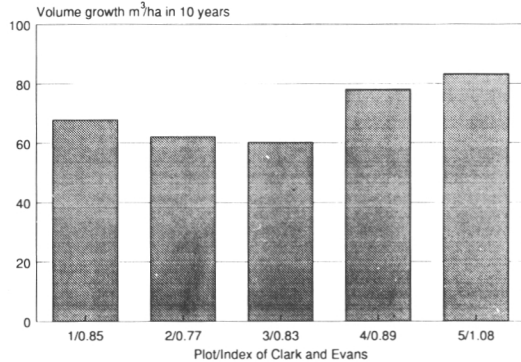

Fig. 8. Predicted stand growth after 5 different thinnings. The crown maps after thinnings are presented in Fig. 7.

5.3 Effect of the width of extraction road on stand growth

The last simulation example studied the effect of the width of extraction road on the growth of a planted Norway spruce stand. The stand basal area was 37.5 m²/ha prior to thinnings, the breast height age 34 years, dominant height 20.1 m and number of stems 2583 trees/ha. The width of the harvest road was 10 m (stand 1), 8 m (stand 2), 6 m (stand 3), 4 m (stand 4) or 2 m (stand 5) and the distance between the roads 30 m (Fig. 9). In all the cases stand basal area was decreased to 25 m²/ha. After cutting the extraction roads, the remainder of the removal was taken systematically according to diameter

starting from the smallest tree (thinning from below).

The grouping indices for the thinned stands were as follows.

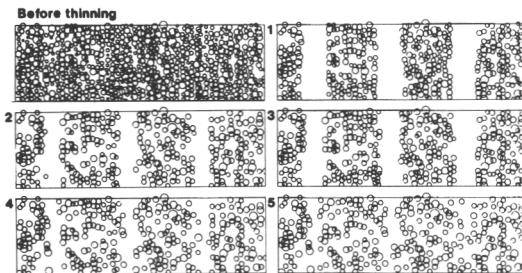| Stand	R	A
1	1.14	1.96
2	1.10	1.51
3	1.12	1.21
4	1.15	0.84
5	1.17	0.61

Fig. 9. Crown map of a model stand before thinning and after 5 different thinnings with varying width of extraction road. The area of the plot is 30 m × 100 m.

As expected, the growth is better the narrower the extraction road (Fig. 10). With 6-m rides the growth is 6.4 % lower than with 2-m rides, and 10-m wide rides decrease the yield by 15 %. In this simulation the growth prediction correlates better with grouping index A (–0.998) than with index R (0.614).
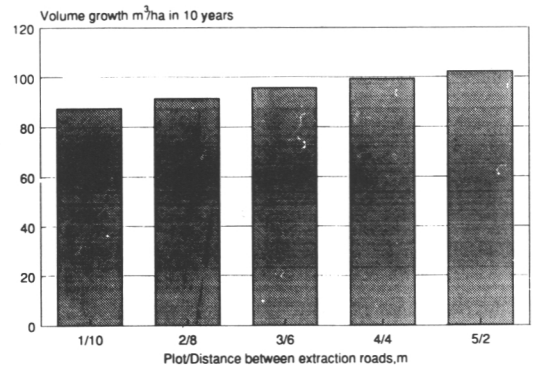

Fig. 10. Predicted stand growth after 5 different thinnings. The crown maps after thinnings are presented in Fig. 9.

6 Discussion

The method for producing model stands, when combined with simulated thinnings, provides a flexible tool for generating material for simulation experiments. The main drawback is that the study material was not variable enough for extreme cases: strictly regular or very irregular stands, or exceptionally young, old, sparse and dense stands. The practical limits for stand characteristics are 300–1500 stems per hectare, 20–80 years for age, 10–35 m²/ha for basal area and 10–28 m for dominant height, and the relationships between these characteristics should correspond to normal Norway spruce stands. Grouping index R should be between 1.40 and 0.80 and grouping index A between 0.35 and 3. Otherwise the predicted tree dimensions may not be reliable. The same limits apply to the spatial growth models. Also within these limits the stand generation method can produce stand basal areas substantially different from the aimed basal area. The produced diameters may there-

fore need scaling to adjust the stand basal area to a specified value.

The obvious way to improve the simulation model is to collect more data, especially from exceptional stands with respect to spatial pattern, site, stand density and age. Uneven-aged stands in the study material would allow the simulation of the yield and development of a selection forest.

The residual variation of the basal area growth model was 0.490 when past growth was not used as a predictor. This compares well with Tham's (1989) much more complicated model where the residual variation was 0.412. The degree of determination of the diameter growth model was 0.595 when past growth was not used as a predictor. In Mielikäinen's (1978) spatial growth model for spruce the degree of determination was 0.435–0.442.

The residual variation of all the presented models were of about the same magnitude as in

the corresponding models of Scots pine (Pukkala 1989a, 1989b). Past growth seems to improve the growth model more with Norway spruce than with Scots pine. Another difference is that spatial predictors do not seem to be equally important for Norway spruce. The advantage of spatial predictors is that, although they do not decrease the residual variation notably, they allow the study of spatial problems.

The small significance of within-stand variation in stand density was also reflected in the diameter models: the correlation between tree diameter and number of stems around the tree was very weak. This, as well as the small contribution of spatial predictors in the growth models, is partly a consequence of the study material: the within-stand variation of the sample plots was small compared to the between-stand variation.

The removal variable (stumps) did not improve the growth models (cf. Mielikäinen 1978). Also the directional distribution of competitors was of small importance. These results are similar to those obtained for Scots pine stands (Pukkala 1989a, 1989b). The reason for the small effect of removal and directional distribution might be that these factors correlate with other variables, and also that the study material did not contain enough variation in these respects.

The models of this study were estimated with an ordinary least squares technique. The shortcoming of the analysis was that observations were not independent of each other because several trees were measured in each plot. An improved model type for this kind of data i a mixed linear model, which divides the stochastic variation in diameter growth into between-stand and within-stand components (Lappi 1986). In this case, the fixed parameters can be estimated using the generalized least squares technique. This type of model can be calibrated by estimating the random stand effects for a particular stand.

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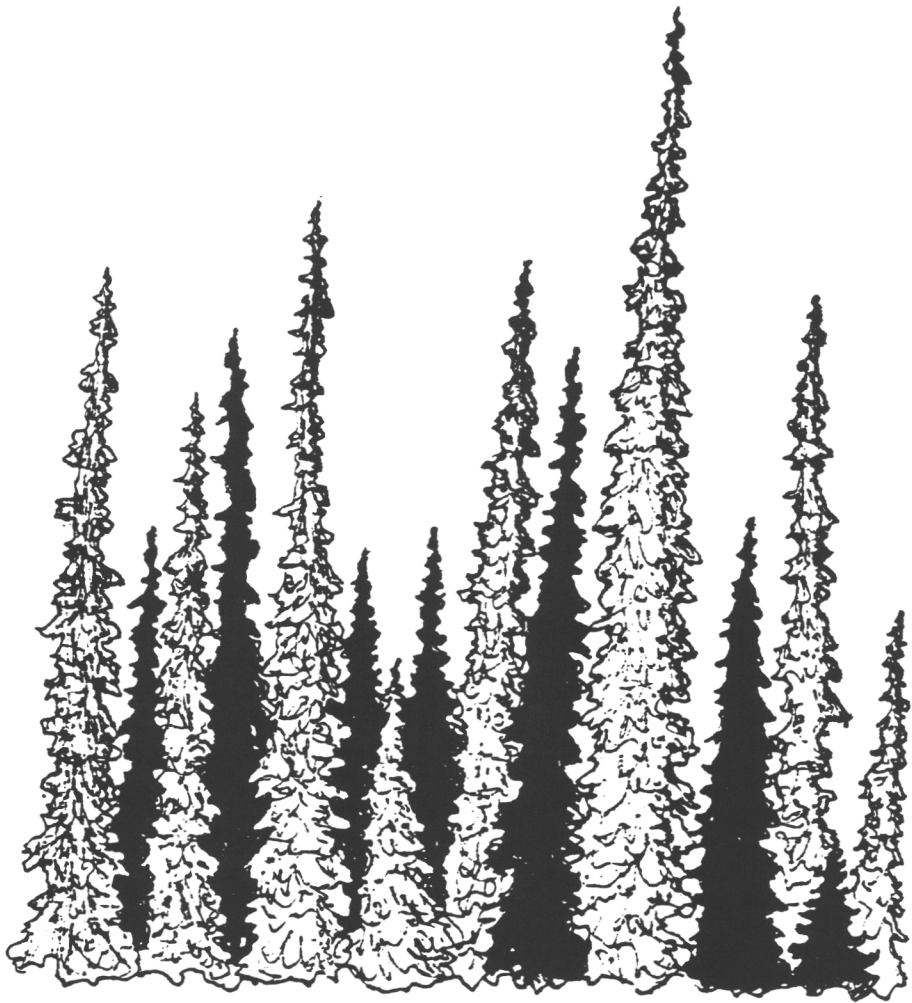
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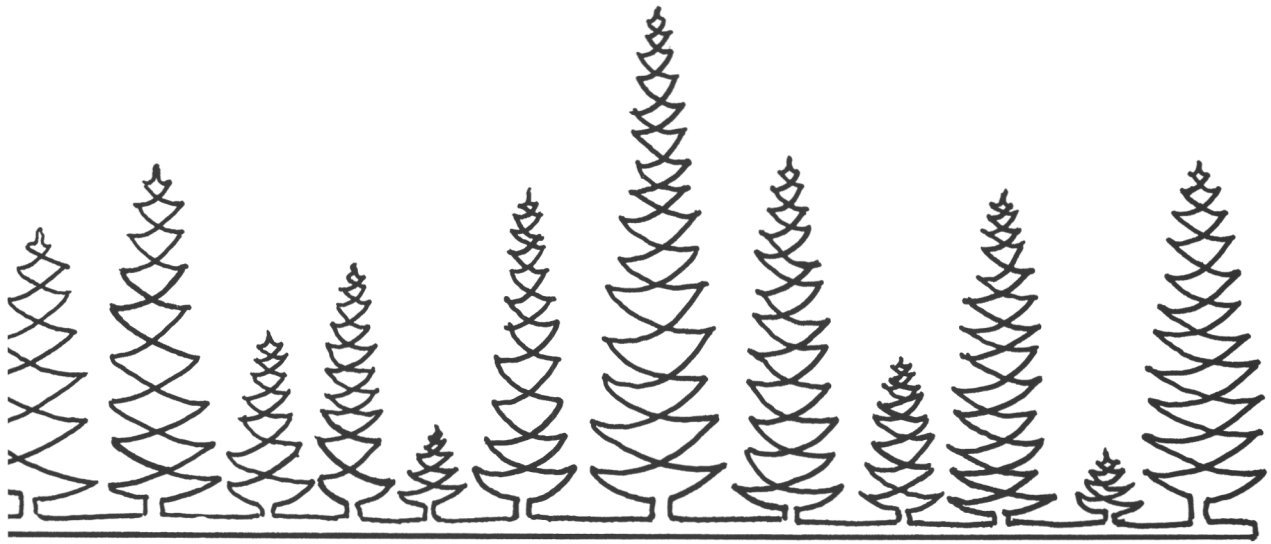
The role of ingrowth in sustaining the structure of an uneven-aged Norway spruce stand

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Abstract

Kolström, T. 1991. The role of ingrowth in sustaining the structure of an uneven-aged Norway spruce stand.

Two different types of models were used to theoretically calculate the required ingrowth to sustain the uneven-aged structure of a Norway spruce (*Picea abies* (L.) Karst.) stand. The model types used were a transition matrix model and a gap model. The ingrowth in the transition matrix model was based on the size of a removed tree and the stand basal area. In the gap model the ingrowth is a result of seedlings abundance and the environmental conditions. The transition matrix model gave more sensible results because the gap size (100 m^2) of the gap model was too small for selection forestry. The calculations showed the ingrowth is of primary importance to the structure of an uneven-aged stand.

Keywords: gap, transition matrix, simulation model, natural regeneration, selection forestry

Introduction

The stand diameter distribution gives the basic information of the stand structure. In uneven-aged stands the diameter distribution is usually described as a reverse J-shaped distribution. The simplest way to describe this diameter distribution is the q-value which is the ratio of stem number between two successive diameter classes (Meyer, 1952). This relationship generates a geometric series of the form:

$$a, \ aq, \ aq^2, \ aq^3, \ ...\ . \tag{1}$$

where a is the number of stems in the largest diameter class and q is the ratio of geometric series.

This emphasizes the number of small trees in a stand and thus, the ingrowth of new seedlings should have an important role in the development of an uneven-aged stand. The ingrowth maintains the uneven-aged structure of a stand. If there are too a few new seedlings in the stand, it will change the diameter distribution, i.e., the structure of a stand slowly changes from uneven-aged to more like even-aged.

Transition matrix models are widely used to describe the development of an uneven-aged stand (see e.g. Usher, 1969; Buongiorno and Michie, 1980; Pukkala and Kolström, 1988). It is attractive because of the simplicity of interpretation and use. The transition matrix model is best suited to selection forestry (Usher, 1971). In transition matrix models, the three basic processes of a stand (birth, growth, and death) are described by a single matrix. Transition matrix models are originally developed for animal population models (Leslie, 1945)

Gap models are also widely used to describe the development of uneven-aged stands (see e.g. Shugart, 1984). Gap models are community dynamics models.

Gap models simulate the annual change in the tree population of a small area of forest, i.e., a gap. Growth increments of single trees, new saplings, and death of trees are calculated. A stand is simulated as arrays of gaps. A gap model incorporates usually a basic set of processess, i.e., light competition, potential tree growth, seedling establishment, and stochastic mortality. In the gap model used the factors affecting growth are light, nutrients, water, and temperature (Kellomäki et al., 1992a).

The aim of this paper is to study theoretically the effect of ingrowth on the future development of an uneven-aged stand. Two different types of models are used in this study to calculate the ingrowth needed to sustain the uneven-aged structure of a Norway spruce (*Picea abies* (L.) Karst.) stand. The model types used are a transition matrix model presented by Pukkala and Kolström (1988) and a process-oriented gap model presented by Kellomäki et al. (1992a; 1992b). The transition matrix model is deterministic whereas the gap model is stochastic.

Methods

The transition matrix model is based on the work of Leslie (1945) and Usher (1966; 1969; 1971). In a transition matrix model describing an uneven-aged stand, the size distribution (e.g. stand diameter distribution) is used instead of the age distribution. New seedlings are born in the gaps left by removed trees. The number of new seedlings correlates with the number and size of trees

removed in thinnings. Thus, the basic form of the transition matrix model is (Usher, 1969)

$$
\begin{vmatrix} h'_1 \\ h'_2 \\ h'_3 \\ h'_4 \\ \cdot \\ \cdot \\ \cdot \\ h'_n \end{vmatrix} = \begin{vmatrix} a_1 & c_2(\lambda-1) & c_3(\lambda-1) & \ldots & c_n(\lambda-a_n) \\ b_1 & a_2 & 0 & \ldots & 0 \\ 0 & b_2 & a_3 & \ldots & 0 \\ 0 & 0 & b_3 & \ldots & 0 \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ 0 & 0 & \cdot & \ldots & a_n \end{vmatrix} \cdot \begin{vmatrix} h_1 \\ h_2 \\ h_3 \\ h_4 \\ \cdot \\ \cdot \\ \cdot \\ h_n \end{vmatrix} \tag{2}
$$

where element h_i ($i=1,2,...n$) is the number of trees in diameter class i at time t_1, h'_i ($i=1,2,...n$) is the number of trees in diameter class i at time t_2, element a_i ($i=1,2, ...n$) is the probability that a tree of the ith diameter class will *remain* in the same class, and b_i ($i=1,2, ...,n-1$) the probability that a tree will *advance* to the nearest larger class during the time interval. The coefficient c_i gives the number of established seedlings born in the gap left by one tree removed from diameter class i and λ is the latent root of the transition matrix.

The transition matrix model used in this study was the same as presented by Pukkala and Kolström (1988) with a few exceptions presented below. The coefficients c_i in the matrix were estimated from the data simulated by the model for natural regeneration by Pukkala (1987). Using the model the number of established seedlings in five years was simulated when a tree belonging to a fixed diameter class was removed (Fig. 1). This data was used to calculate the following equation which gives the dependence of coefficient c_i on the stand density and the size of a removed tree:

$$
c_i = 0.028443 \cdot d_i^2 - 0.115461 \cdot G \tag{3}
$$

where c_i is the coefficient of diameter class i; d_i is the midpoint of diameter class i (cm) and G is stand basal area (m^2 ha^{-1}).
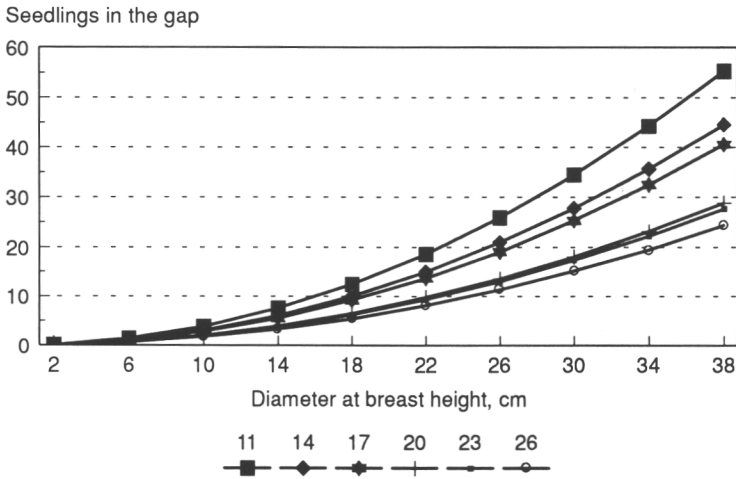
Seedlings in the gap

Figure 1. Dependence of the number of seedlings established on the gap of a removed tree during five years and the stand density. Legend labels indicate the stand basal area (m² ha⁻¹). Calculations based on the model of Pukkala (1987).

The gap model used in this study is described in detail by Kellomäki et al. (1992a; 1992b). The model is stochastic and simulates the dynamics of an area of 100 m² several times. The growth and development of trees are controlled by temperature and light conditions, and the availability of nitrogen and water. The natural regeneration of trees is divided between seeding and sprouting. The seeding process produces seedlings as follows:

$$NPLANT = SEEDMX \cdot Y_I \cdot Y_T \cdot Y_W \cdot YFL \qquad (4)$$

where *SEEDMX* is the potential number of seedlings (1 ha⁻¹), Y_I, Y_T, and Y_W are the growth multipliers (light, temperature, and water, respectively), and *YFL* is an uniformly distributed random number between 0 and 1. The model was modified to have ten different height classes instead of original four, to be able to simulate selection cuttings.

Simulations

The basal area of the simulated Norways spruce stand was 19.5 m^2 ha^{-1} and the stocking was 3 209 trees ha^{-1} including seedlings (Table 1). The stand diameter distribution has the q-value 1.6 which is typical for uneven-aged stands (Alexander and Edmister, 1977).

Table 1. Stand diameter distribution used in the simulation examples. The diameter class -2 cm represents seedlings (height less than 1.3 m).

Class midpoint (cm)	Number of trees ha^{-1}	Class midpoint (cm)	Number of trees ha^{-1}
-2	1210	22	72
2	756	26	45
6	473	30	29
10	295	34	18
14	185	38	11
18	115		

The level of regeneration was varied by multiplying the c_i parameter of the transition matrix model or applying multipliers to the *SEEDMX* parameter in the gap model. The used multipliers were 0.01, 0.1, 0.5, 0.75, 1.0, 1.25, 1.5, and 2.0 in both models. The simulation time was 100 years.

In the transition matrix model the stand was thinned every five years using the sustainable harvest proportion, an intensity indicated by the latent root (λ). The thinning intensity was equal for all diameter classes. In the gap model the stand was thinned every 10th year by cutting 20% of the number of stems from every height class. The number of iterations was 11 in the gap model.

The stand basal area at the end of the simulation period increased along the increased regeneration multiplier in both models (Fig. 2A). The change was more clear in the matrix model than in the gap model. The total removal

during the whole simulation period decreased slightly when the regeneration multiplier increased in the matrix model (Fig. 2B). In the gap model the removal increased with the regeneration multiplier. The total amount of removal was very low in the gap model in spite of the cutting proportion of 20 % compared to that of the matrix model.

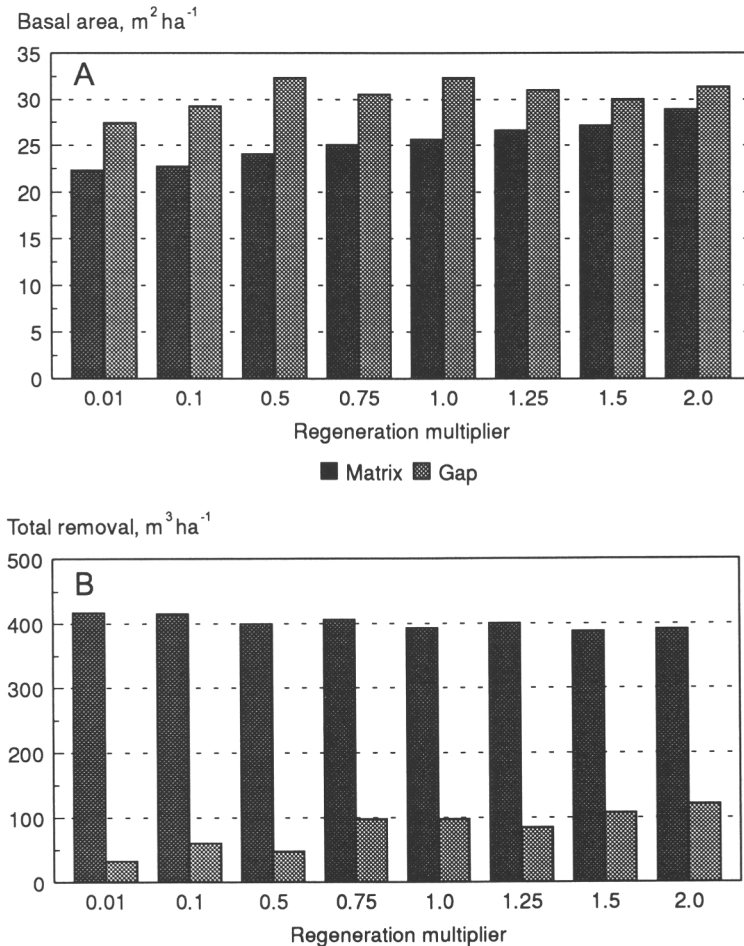Basal area, $m^2 ha^{-1}$

Total removal, $m^3 ha^{-1}$

Figure 2. Dependence of the stand basal area after 100-year simulation period (A) and total removal during the simulation (B) and the regeneration multiplier by the used models. (Note the nonlinear x-axis).

The effect of the regeneration multiplier on the stand diameter distribution at

9

the end of the simulation was clear (Fig. 3). This effect was more clear with the matrix model (Fig. 3A) than with the gap model (Fig. 3B) because of the variation in the results of the gap model. They indicate the stochasticity of the gap model. The number of trees in the smallest diameter class in the gap model is noticeable low (Fig. 3B).
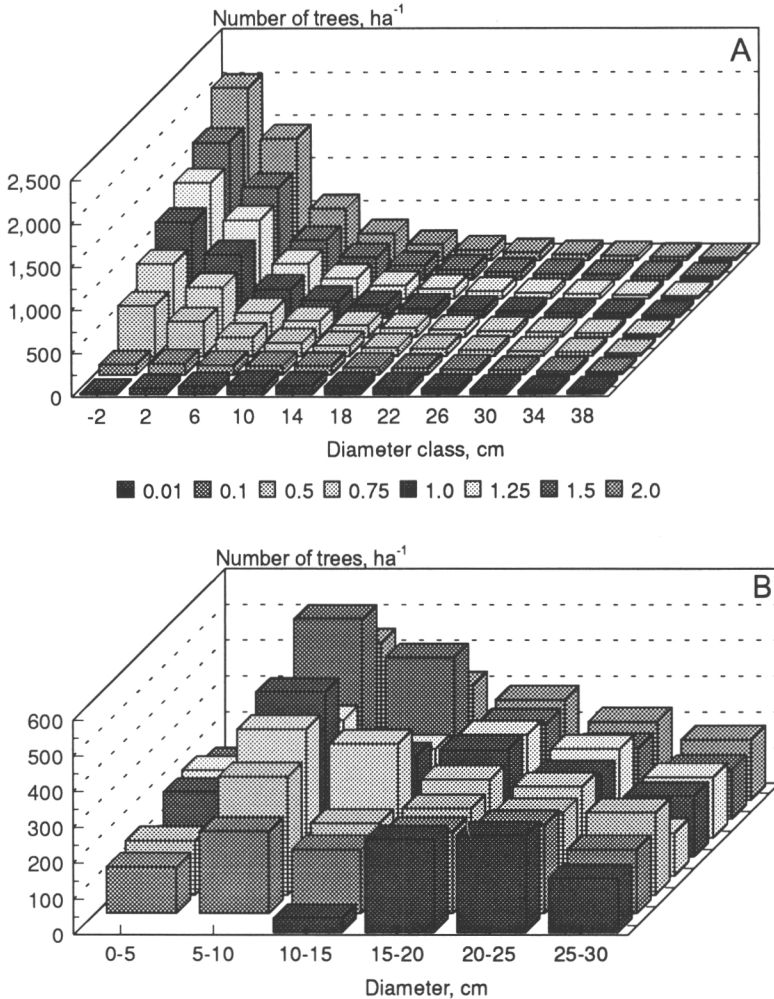
Figure 3. Dependence of the stand diameter distribution after 100 years simulation (A = matrix model, B = gap model) and the regeneration multiplier. Legend labels indicate the regeneration multiplier.

The number of seedlings was near to that of the initial stand when the

regeneration multiplier had a value of 1.1 in the matrix model (Fig. 4; Table 1). The number of trees in the diameter class of 2 cm is also very near to the initial value. The difference between the initial and the final stand in the frequencies of diameter classes is small in all diameter classes (Fig. 3; Table 1).

Figure 4. Dependence of the number of seedlings (trees height less than 1.3 m marked as DBH -2 cm) and number of trees in the diameter class 2 cm (DBH 2 cm) after 100 years simulation and the regeneration multiplier. (Note the nonlinear x-axis).

Discussion

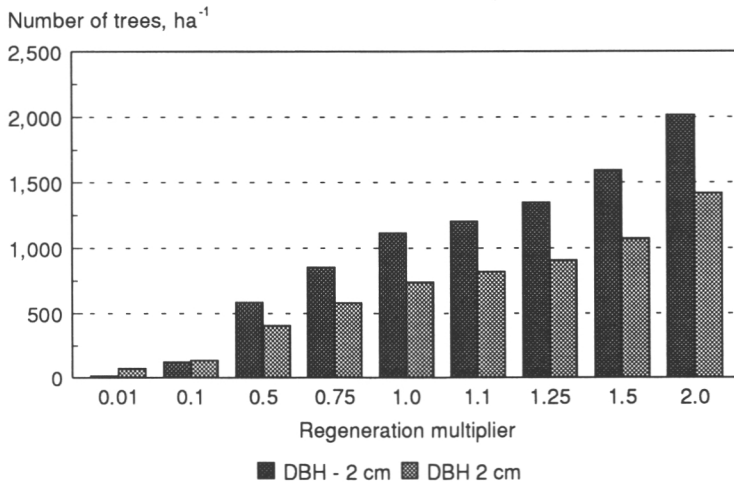The general framework and the regeneration part for the models used are presented in this paper. The more detailed description of the models as well as the validation of the models are presented in the papers of Pukkala and Kolström (1988) (matrix model) and Kellomäki et al. (1992a; 1992b) (gap model). The gap model was modified to have more height classes. This was done because of the selection thinnings. The regeneration coeffiecients c_i of the matrix model were estimated from the simulated data. This was done because there was not suitable data available about the regeneration of uneven-aged Norway spruce stands. This lack of empirical data causes difficulties to check the validity of the regeneration model used (see Pukkala, 1987).

The gap models are widely used to simulate the long-term development of forest stands (West et al., 1981; Shugart, 1984). The gap size is critical in determining the type of simulated forest dynamics (Leemans and Prentice, 1987). Gap-phase dynamics is simulated if the size of simulated gap is the maximum crown area of the largest trees (Shugart and West, 1979). In the gap model used the size of the gap was 100 m^2. This gap size is well suited to simulate the natural development of Norway spruce stands (Prentice and Leemans, 1990) as well the development of even-aged stand. However, it seems that the gap size might be too small to reveal reliably the effects of selection forestry. Thinnings in simulations are unreliable with large trees because there are only a few big trees in the simulated gap when the sustained harvest proportion is usually between 5 and 20 % from the number of stems in each height class.

Transition matrix models are often used to study different treatment possibilities of uneven-aged stands (see e.g. Usher, 1966; Buongiorno and Michie 1980; Rottier, 1984), as well as to predict the growth of even-aged stands (Sallnäs 1990). The matrix model used supposed that each size-class is thinned according the sustainable harvest proportion. In the calculations presented the

sustainable harvest proportion is used always. The new seedlings are born into the gaps left by removed trees. This assumption does not consider the shade-tolerant feature of Norway spruce as a tree species (Kalela, 1949; Schmidt-Vogt, 1986).

Both models react in the same way to a change in the level of ingrowth. Especially the diameter distribution after the 100-year simulation period was quite similiar with one exception. The number of trees in smallest diameter class after simulations was low in the simulation runs of the gap model. Thus, there was no longer a reverse J-shaped diameter distribution. In the transition matrix model a rough reverse J-shaped diameter distribution was left except in the runs with very low regeneration level (0.01 and 0.1).

The matrix model gave results with less variation compared to the gap model. The small gap size in respect to the thinnings is one reason for the illogical variation in the results of the gap model. The difference in the nature of the models (stochastic vs. deterministic) is another reason. The stochasticity in the regeneration of the gap model takes into consideration the wide variation between different years in results of the regeneration process of Norway spruce (Koski and Tallqvist, 1978; Valtanen, 1988).

The simulation results indicated the importance of the level of regeneration which is needed to sustain the structure of an uneven-aged stand. It should be mentioned, however, that these calculations are theoretical and more reliable parameters need empirical measurements especially for the transition matrix model. The gap model need further development in the thinning methods. On the other hand, the calculations emphasized the importance of regeneration to selection forestry.

Acknowledgements

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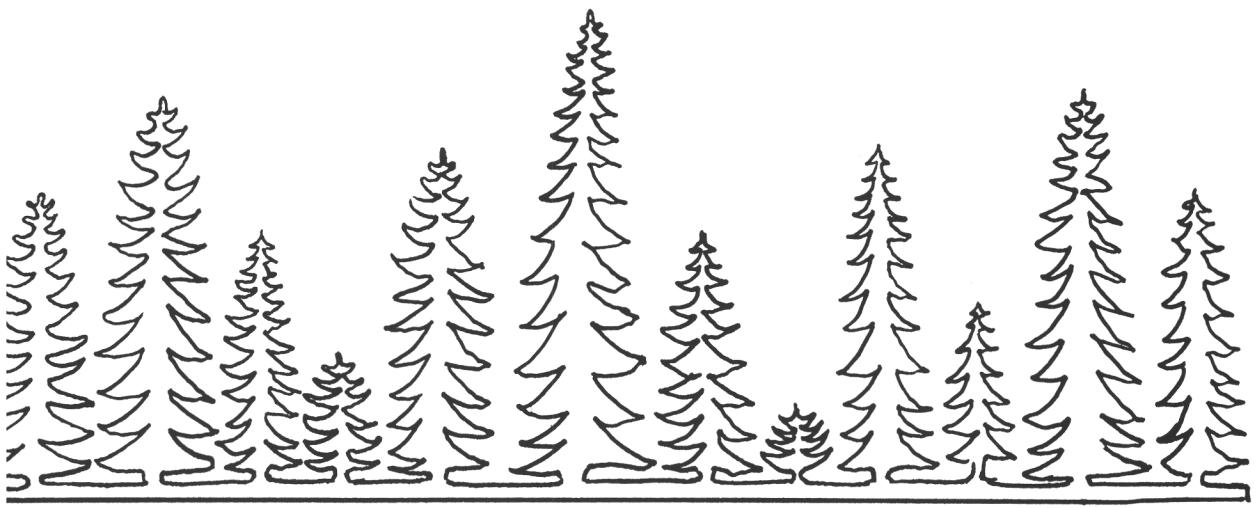
Modelling the development of an uneven-aged Norway spruce stand

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Abstract

Kolström, T. Modelling the development of an uneven-aged Norway spruce stand.

A transition matrix model of an uneven-aged Norway spruce (*Picea abies* (L.) Karst.) stand is presented. The transition probabilities are based on material from 48 study plots in eastern Finland. The ingrowth of the transition matrix is based on material from 8 study plots and on previous studies. In the model runs the sustainable harvest proportion for 5 years varied between 7 and 20 % of the stocking depending on the stand basal area. The shape of the stand diameter distribution had no notable effect on the sustainable harvest proportion. The extension of the thinning interval from 5 to 10 years slightly reduced the total removal during the simulation time.

Keywords: *Picea abies*, transition matrix, selection forestry, simulation model

Introduction

The diameter distribution contains basic information about stand structure. In an uneven-aged stand the diameter distribution is usually described as a reverse J-shaped distribution or, more shortly as a J-shaped distribution. Mathematically a reverse J-shaped diameter distribution can be presented as a negative exponent function or as a Weibull-distribution. The simplest way to describe the diameter distribution is the so-called q-value which is the ratio of stem number between two successive diameter classes (Meyer, 1952). This relationship generates a geometric series of the form:

$$a, aq, aq^2, aq^3, ... \qquad (1)$$

where a is the number of stems in the largest diameter class and q the ratio of geometric series.

The natural development of a stand consists of birth, growth, and death of trees. Of these three processes the main processes in treated stands are birth and growth, harvesting reducing the importance of death. In an uneven-aged stand these processes are simultaneous whereas in an even-aged stand they occur more in sequence. In simulation models they are usually mimiced separately.

In transition matrix models these three basic processes are described by a single transition matrix (Jeffers, 1982; Swartzman and Kaluzny, 1987). In a transition matrix model describing an uneven-aged stand, the size distribution (e.g. diameter distribution) is used instead of age distribution (Leslie, 1945;

Usher, 1971). The basic form of the transition matrix model for selection forest is (Usher, 1969a):

$$
\begin{vmatrix} h'_1 \\ h'_2 \\ h'_3 \\ h'_4 \\ \cdot \\ \cdot \\ \cdot \\ h'_n \end{vmatrix} = \begin{vmatrix} a_1 & c_2(\lambda\text{-}1) & c_3(\lambda\text{-}1) & \ldots & c_n(\lambda\text{-}a_n) \\ b_1 & a_2 & 0 & \ldots & 0 \\ 0 & b_2 & a_3 & \ldots & 0 \\ 0 & 0 & b_3 & \ldots & 0 \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ 0 & 0 & \cdot & \ldots & a_n \end{vmatrix} \cdot \begin{vmatrix} h_1 \\ h_2 \\ h_3 \\ h_4 \\ \cdot \\ \cdot \\ \cdot \\ h_n \end{vmatrix} \qquad (2)
$$

where element h_i ($i=1,2,...n$) is the number of trees in size class i at time t_1, h'_i ($i=1,2,...n$) is the number of trees in size class i at time t_2, element a_i ($i=1,2, ...n$) is the probability that a tree of the ith size class will *remain* in the same class, and b_i ($i=1,2, ... n\text{-}1$) the probability that a tree will *advance* to the nearest larger class during the time interval. The coefficient c_i gives the number of established trees born in the gap left by one tree removed from class i.

If the stand has a diameter distribution corresponding to a latent vector, the latent root λ describes directly the rate of increase of the population. The harvest level (H) that keeps the population constant is $(\lambda\text{-}1)/\lambda$. If this proportion is harvested from every diameter class during the time step, the stand remains unchanged and can be regarded as stable (Usher, 1969b, 1971; Pukkala and Kolström, 1988). In the calculation of regeneration, it is assumed that each size-class is thinned according the sustainable harvest proportion (H) once during every time interval.

Pukkala and Kolström (1988) developed further the transition matrix model by making the transition probabilities dependent of stand density and adding a so-called waiting class for trees shorter than 1.3 m. In their model, however, transition probabilities are based on the growth models for even-aged stands. Regeneration parameters are not based on measurements in uneven-aged stands.

Additionally, deviation in cuttings from the sustainable harvest proportion brings errors in the calculation of regeneration.

The aims of this study are (i) to develope the transition matrix model to describe the development of an uneven-aged Norway spruce (*Picea abies* (L.) Karst.) stand and (ii) to study the effect of regeneration, thinning intensity, and thinning interval on the development of uneven-aged stands.

Material and methods

Transition probabilities

The transition probabilities were calculated from 48 plots measured in Norway spruce (*Picea abies* (L.) Karst.) stands in eastern Finland (about 62°N, 30°E, 100-120 m asl.). The plot size varied according to stand density; the number of trees more than five meters from the nearest plot edge was 40-200 in each plot. The stand age, density, and spatial distribution of trees varied considerably (Appendix 1). The site fertility was either good (*Oxalis-Myrtillus* type) or medium (*Myrtillus* type) in Finnish classification. The time since previous thinning was at least five years. Stands were either plantations or naturally regenerated.

Tree diameter and coordinates were measured for each tree and stump. Height and the annual radial growth of the past 10 years were measured for the trees more than five meters from the plot edge. If height was not measured, it was predicted from diameter by a model based on the measured heights and diameters. Age and diameter growth were measured on a core taken at breast height. If the core was unclear, the age was predicted from diameter.

To predict future growth, tree diameters five years earlier were derived. Transition probabilities for each diameter class (4-cm diameter classes) in each plot were calculated for a five-year period. These data were used to calculate the following equation:

	Coeffiecient		Predictor	t-value
$b_i =$	+0.035936	·	$\ln(d_i)$	1.8209
	+0.181339	·	$\ln(H_g)$	6.5498
	-0.010495	·	G	-4.4669

where b_i is the transition probability of class i ($i=2,...n$); d_i is the midpoint of

class i (cm); H_g is the mean height of the stand (m) and G is the stand basal area (m^2 ha^{-1}). The F-value of the equation is 177.532 (3,385), degree of determination 0.578, and standard error of estimate 0.316.

The element b_1 is the share of small trees (height < 1.3 m) that will grow up to the next size-class during the 5-year period. The element a_1 is the part of the small trees that remain in the same class; the rest of small trees, i.e., $1-(a_1+b_1)$ will die. These parameters were estimated based on the works of Cajander (1934), Bergan (1971), and Sandvik (1986). Parameter a_1 was assumed to be x to the power of 5 (x^5), where x is the annual average proportion (weighted by the number of seedlings) of seedlings staying alive during the first 11 years of stand development (see Fig. 1). Thus, the element a_1 was set to 0.435. According to Cajander (1934) and Bergan (1971) trees having height 80 cm will reach the height of 1.3 m in 5 years. Small spruces reach the height of 80 cm in 10 years (Cajander, 1934). Thus, based on the mortality among seedlings given by Sandvik (1986) the element b_1 was set to 0.221.
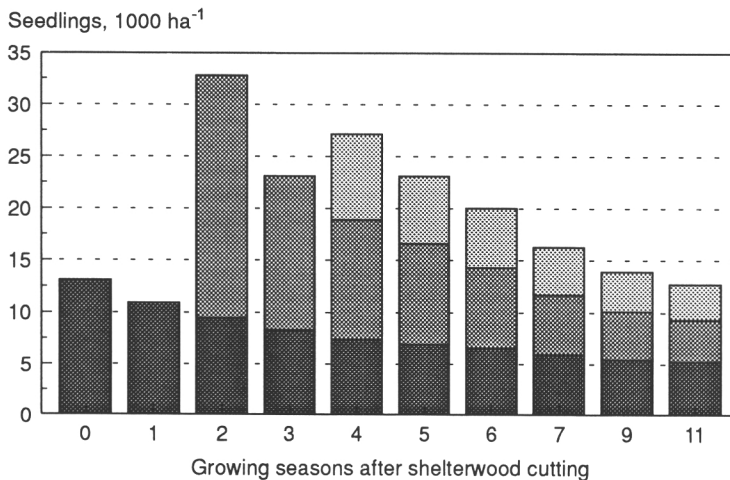

Figure 1. Mortality among seedlings from three different seed years (Redrawn from Sandvik 1986).

Regeneration parameters

The values c_i of the transitition matrix indicate how many new seedlings can appear in the gap left by one harvested tree. In the calculation of the number of gaps the weighted average of the thinning proportion of previous time interval and the sustainable harvest proportion H was used. The thinning proportion was weighted by 0.7 and the sustainable harvest proportion by 0.3.

The regeneration model was estimated from the data of 8 plots of Norway spruce stands in eastern Finland. All the plots were thinned 7 - 11 years ago. In thinnings, trees had been removed from all diameter classes. The establishment of new seedlings were measured as follows.

All the seedlings (between 0.1 - 4.0 m in height) were measured with the same method as used for trees (previous 48 plots), thus location, diameter at breast height, height, and time of birth (before or after thinning). Seedlings shorter than 10 cm were recorded in 4 m^2 sample plots, which were in a grid of 5 m $\cdot$ 5 m over the plot. Age and height were measured for these small seedlings. Based on this material the number of seedlings born during the past five years was calculated (see Table 1). The same method was used in seven test plots measured in southern Finland (Table 1).

The number of established seedlings varied greatly and there was no clear dependent variable to describe this variation. Therefore average of these 8 plots (0.566 seedlings m^{-2}) was used in the calculation of regeneration parameters. The parameter c_i was thus directly related to the size of gap left by a removed tree.

Table 1. Stand characteristics of the study plots used in calculating regeneration parameters.

Study plots	N 1 ha^{-1}	G m^2 ha^{-1}	H$_g$ m	D$_g$ cm	Seedlings 1 ha^{-1}
1	508	16.5	13.3	17.9	2 151
2	567	19.7	15.1	18.7	14 453
3	722	17.5	12.4	15.8	100
4	983	18.3	11.0	14.1	3 333
5	783	24.0	14.8	17.5	11 833
6	650	23.6	14.6	19.1	4 887
7	5ɔ0	19.5	12.6	17.5	892
8	1 160	25.5	11.7	14.0	26 518
Test plots					
1	2 212	22.4	17.3	23.3	28 515
2	2 468	19.9	17.5	22.4	23 790
3	1 481	16.9	21.3	27.9	28 555
4	1 431	17.3	18.0	22.0	38 788
5	980	12.5	16.6	21.2	28 125
6	2 313	14.3	17.9	22.8	352
7	2 556	19.4	20.7	22.6	2 852

N = Number of trees, 1 ha^{-1}, G = Stand basal area, m^2 ha^{-1}, H$_g$ = Mean height, weighted by basal area, m, D$_g$ = Mean diameter, weighted by basal area, cm.

Sensitivity analysis

The regeneration parameters of the model were estimated based on a small amount of data as regards to the stochasticity. Thus, the sensitivity of the model to the regeneration parameters was tested. The initial basal area of the simulated Norway spruce stand was 19.5 m^2 ha^{-1} and the stocking density was 3 198 trees ha^{-1} including seedlings. The diameter distribution of the stand has the q-value of 1.6. The simulation time was 100 years and the stand was thinned during every time step by removing 16 % of the stems in every diameter class. The thinning intensity was the sustainable 5-year removal for the initial situation. This diameter distribution and basal area are called the standard stand and the described simulation, the standard run.

The level of the regeneration was changed by multiplying the c_i parameter with 0.01, 0.1, 0.5, 0.75, 1.0, 1.25, 1.5, and 2.0. The effect of the level of regeneration was quite linear (Fig. 2A). The change of ±25 % in the regeneration level caused the change of 17-18% in the stand basal area after 100-year simulation compared to the standard run. The effect of regeneration level was stronger when the multiplier decreased than when the multiplier increased. As a result of the low regeneration level the J-shape of the diameter distribution almost disappeared during the simulation (Fig. 2B).

The effect of parameters a_1 and b_1 on the stand development was studied separately. The value of both parameters was changed ±10% and ±20% from the original value. The effect of both elements was linear. The element a_1 had a minor effect. A decrease of 20 % decreased the stand basal area by 9% compared to the standard run (Fig. 3). The element b_1 had more effect on the result. A change of -20% in the value of b_1 resulted in 18 % decrease in the final stand basal area.
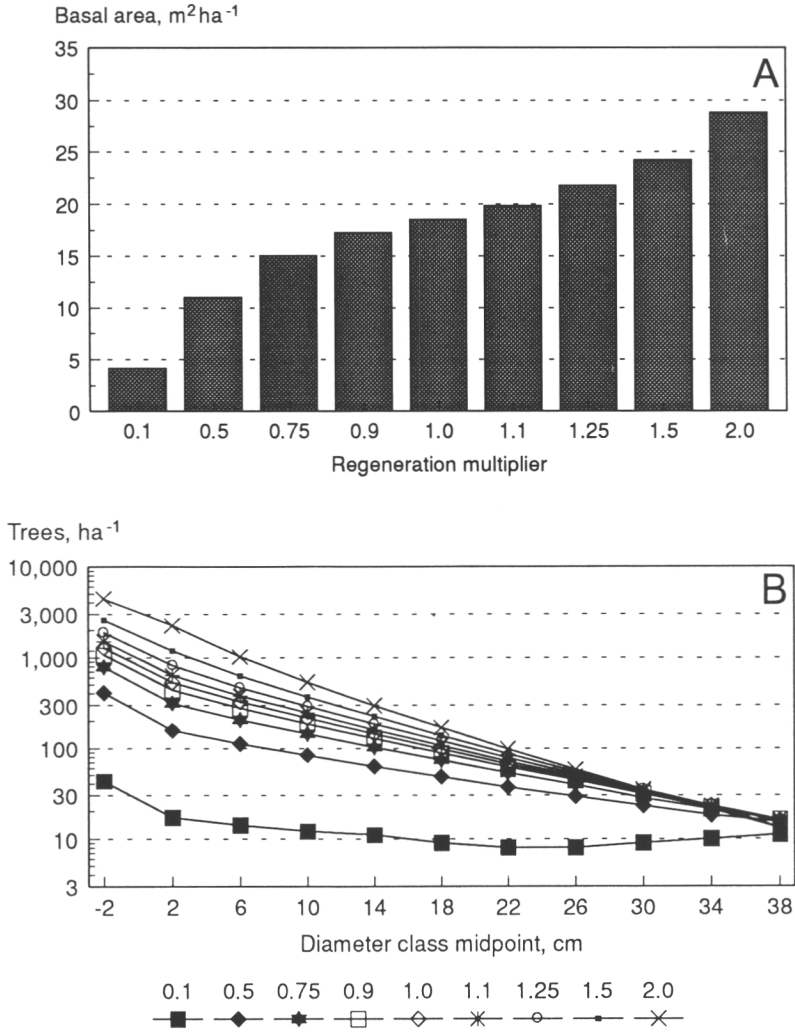
Basal area, m² ha⁻¹

Figure 2. The effect of the regeneration multiplier on the stand basal area (A) and diameter distribution (B) after the 100-year simulation. (Note the nonlinear x-axis in A and y-axis in B).

Basal area, m^{2}ha^{-1}
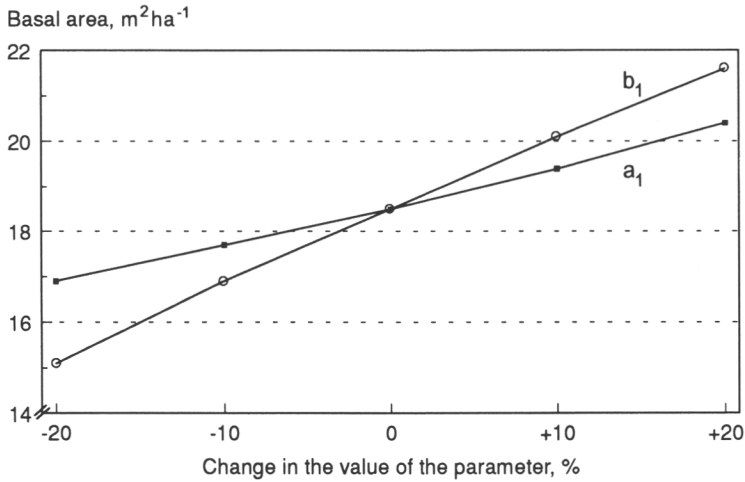
Figure 3. The effect of the elements a_1 and b_1 on the stand basal area after the 100-year simulation.

Simulation examples

The dependence of the sustained harvest proportion (i) on the stand basal area and (ii) on the shape of the diameter distribution were calculated for an uneven-aged stand. The q-value was varied between 1.4 and 1.8. The value 1.6 is typical for uneven-aged stands (Alexander and Edmister, 1977). The sustainable harvest proportion (5-year time step) varied from 7 to 20 % depending on the stand basal area (Fig. 4). In dense stands the sustainable harvest proportion was lower than in sparse stands. The shape of the diameter distribution had only a minor effect on the sustainable harvest proportion.

Sustainable 5 year removal, %

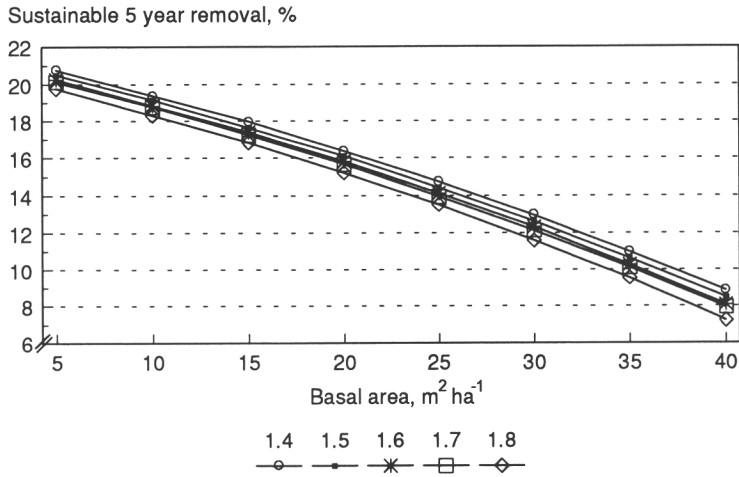Figure 4. Dependence of the sustainable harvest proportion on the stand basal area and structure. The stand structure is described by the q-value.

The effect of thinning interval and intensity was examined in the second example. The simulated thinning proportions of 15, 20, 25, 30, and 35 % were removed from each diameter class. The initial stand was the standard stand. The thinnings were made at 5, 10, or 15 years intervals. The simulation time was 90 years. When thinning was made in every time step (i.e., every 5 years) the harvesting proportion of over 15 % decreased the stand basal area after the simulation compared to the initial stand basal area (Fig. 5). If the thinnings were made every 10 years the harvesting proportion could be increased up to 25 % without decrease in the basal area after the simulation. The difference between thinning intervals of 10 and 15 years was smaller than the difference between 5 and 10 years (Fig. 5).

Basal area, m^{2}ha^{-1}

Thinning proportion, %

■ 5 years ▨ 10 years ▨ 15 years
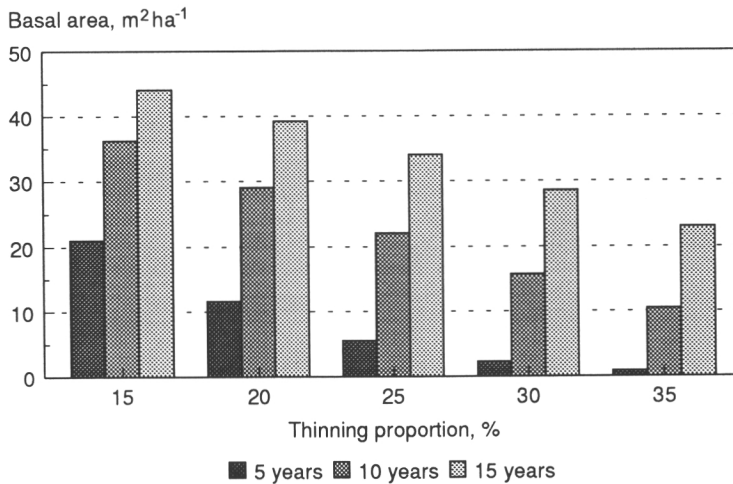
Figure 5. The effect of thinning proportion and interval on the stand basal area after 90 years simulation.

The maximum total removal during the simulation was 740 m^3 ha^{-1} (Fig. 6). This removal was obtained when the thinning intensity was 15 % and time interval 5 years. When the time interval was 10 years high total removals were received with the thinning intensities of 25 % and 30 % (over 700 m^3 ha^{-1}). These cases were the same where the stand basal area at the end of the simulation was near the initial stand basal area, i.e., 19.5 m^2 ha^{-1} (Fig. 5).

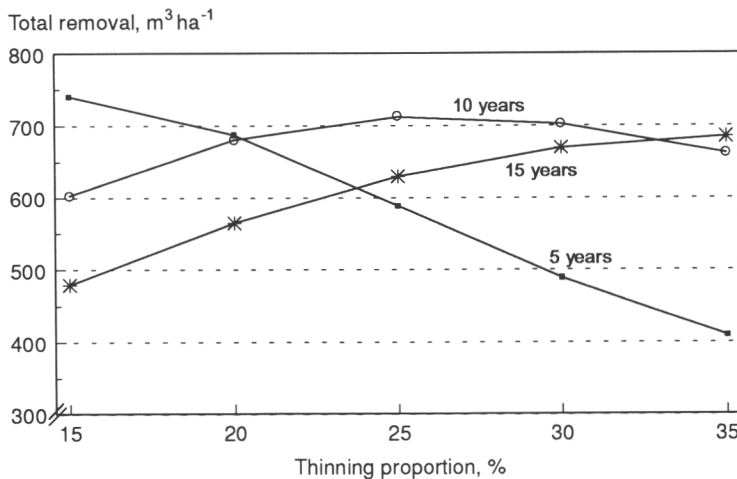Total removal, m^{3}ha^{-1}

Thinning proportion, %

Figure 6. The effect of thinning proportion and interval on the total removal during the simulations.

Discussion

In the presented transition matrix model for Norway spruce most of the parameters were based on empirical measurements (transition probabilities, regeneration parameters) and a few parameters on previous studies (a_1, b_1). The stands used to estimate transition probabilities represent Norway spruce stands in eastern Finland (about 62°N, 30°E, 100-120 m asl.). There is a large variation in the spatial distribution of stands, density, mean diameter, and basal area of the stands (Appendix 1). Although this variation is wide, only a few stands are in a strict sense uneven-aged, rather they are uneven-sized stands. Some of the stands are even-aged plantations. Using this type of data, it is possible to use the model to describe the development of stands that are also between even and uneven-aged stands.

The transition probabilities were tested by using plots 2, 22 and 32 as an independent test material. The model was re-estimated from the rest of the 45 plots. The model frequently overestimated the transition probabilities of small diameter classes and underestimated those of large diameter classes (Table 2). However, there is a wide variation in the measured transition probabilities of the same diameter class between the test plots. In larger plots the variation decreases and the estimated transition probabilities would be nearer to the measured one.

The transition probabilities were quite high compared to earlier studies (Pukkala & Kolström, 1988). Thus, the sustainable harvest proportion was high, i.e., between 7 and 20 % of stocking depending on the basal area of the stand. The annual growth varied from 2 up to 8 m^3 ha^{-1} corresponding quite well to the growth of treated Norway spruce stands in southern Finland (see e.g. Koivisto 1954; Nyyssönen and Mielikäinen, 1978). One reason for high transition probabilities was that most of the stands were treated before the measured period.

Table 3. The measured (m) and estimated (e) transition probabilities of three study stands. The transition probabilities were estimated from the rest 45 stands.

Class mid-point, cm	plot 2		plot 22		plot 32	
	m	e	m	e	m	e
2			.727	.302	.111	.325
6			.167	.341	.211	.363
10	.000	.294	.500	.359	.125	.381
14	.333	.306	.500	.371	.385	.393
18	.778	.315	.667	.380	.375	.402
22	.417	.322	.500	.387	.222	.409
26	.200	.328	1.000	.393	.500	.415
30	.667	.333			.667	.425
34			1.000	.403		
38			.000	.406	.000	.429

The used modelling approach presupposes that site productivity is constant. However, Sirén (1955) showed that growing Norway spruce stand over a very long time-span may cause a deteriation in the productivity and regeneration capability of the site. This fact causes uncertaintity in the long-term simulations.

The reverse J-shaped diameter distribution affected the growth because most of the trees belonged to small diameter classes. This situation corresponds to the situation in selection forestry where cuttings are repeated at certain intervals. The diameter had a slight positive correlation with the transition probability. Similiar effect was found by Spiecker (1986). In the study of Lundqvist (1989) the diameter increment was equal in all diameter classes.

The regeneration coefficients c_i were based on the mean value of established seedlings ha^{-1} on the measured plots. The variation between measured plots was very high; the minimum was 100 new seedlings ha^{-1} in five years and the maximum over 26 000 new seedlings ha^{-1}. The same phenomenom can be seen

also in the test plots. However, the mean value in these data was clearly lower than that of the test plots. The test data was not from the same geographical area.

The number of new seedlings did not negatively correlate with the stand basal area. This agrees with Lundqvist (1989), who found out that stand density did not affect seedling abundance. The regeneration data and the test plots indicate a high stochasticity in the regeneration process of a Norway spruce stand (see also Sarvas, 1944; Koski and Tallqvist 1978; Valtanen, 1988). In the calculation of the number of gaps the weighted average of simulated thinning proportion and sustainable harvest proportion was used. In this way, it is possible to describe the regeneration characteristics of Norway spruce as a shade-tolerant tree species (Schmidt-Vogt, 1986).

The elements a_1 and b_1 in the transition matrix were estimated based on Cajander (1934), Bergan (1971), and Sandvik (1986). These studies dealt with shelterwoods stands of Norway spruce. Lundqvist (1989) estimated that the time needed by seedlings to develop from 0.1 m to 1.29 m is from 24 to 47 years. However, data was not available data on the initial development of seedlings in uneven-aged stands. Sensitivity analysis pointed out the importance of the parameter b_1.

The 5 years' sustainable harvest proportion gave removals between 10 and 40 m^3 during the time step (5 years) depending on the stand volume. The simulation results indicate that the thinning interval can be extended up to 10 years with a thinning proportion of 25 or 30 % with only small losses in the total removal. In that way, the thinning removal could be increased up to 80 - 100 m^3 ha^{-1}. Solomon and Frank (1983) showed that the harvest interval had only a slight effect on the growth of an uneven-aged stand. Spiecker (1986) recommended that removals should be done often and modest.

The transition matrix model assumes that the trees whose diameter is over 40

cm are harvested automatically. This removal is under 10 % of the total removal in these simulations. The use of the thinning intervals of 10 and 15 years presupposes the use of corresponding time step in the model.

The harvest proportion was kept the same in all size classes. This is not always the optimal way to thin selection forests. Therefore, mathematical optimization should be used to find the best structure, thinning interval, and intensity for selection forests (Buongiorno and Michie, 1980). Anyway, the most important part of the future work is to consider the wide stochasticity of the regeneration process.
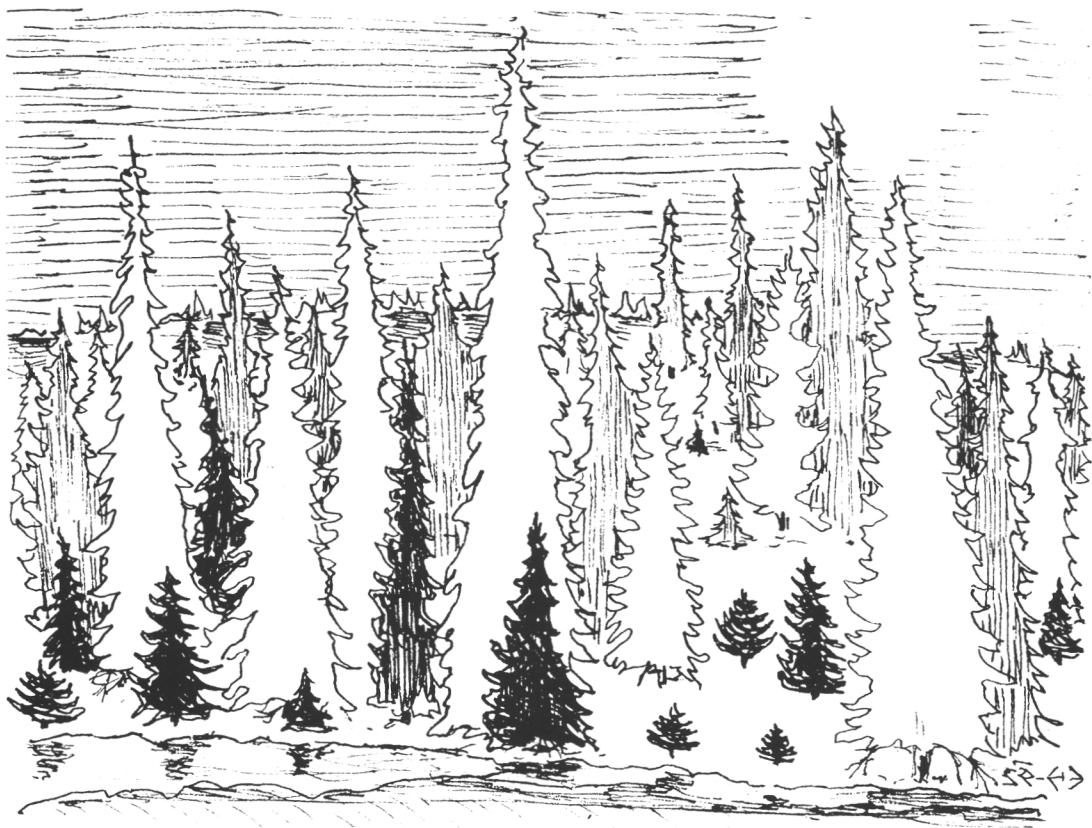
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Appendix 1. Stand characteristics of the study plots. For definitions of symbols, see Table 1. Parameters R and A are the grouping indices of Clark and Evans, and Hopkins, respectively.

Plot	N ha^{-1}	G m^2 ha^{-1}	T_g a	H_{dom} m	D_g cm	H_g m	R	A
1	1592	41.0	42.7	22.6	23.5	18.0	1.27	0.64
2	767	35.0	37.4	21.8	25.6	19.6	1.30	0.55
3	700	19.8	34.9	20.4	21.6	18.2	1.48	0.35
4	660	24.4	36.3	20.7	23.1	18.8	1.14	0.80
5	1038	10.8	16.5	11.1	18.9	9.1	1.31	0.80
6	884	19.3	29.3	19.2	22.8	15.4	1.22	0.75
7	606	21.3	70.6	26.2	26.6	21.0	1.23	0.67
8	167	16.4	70.5	25.2	39.5	24.1	1.34	0.51
9	550	21.2	41.2	21.4	23.4	18.8	1.43	0.36
10	411	20.6	38.9	22.4	27.8	20.5	1.23	0.58
11	167	14.7	77.8	25.6	37.1	24.3	1.38	0.52
12	988	28.1	40.1	21.3	21.6	18.0	1.36	0.70
13	455	24.7	38.1	21.4	28.0	19.7	1.24	0.55
14	619	21.2	42.0	20.0	22.0	18.5	1.29	0.42
15	934	13.4	15.4	11.2	15.3	10.4	1.20	0.98
16	207	10.5	66.1	22.8	35.8	20.8	1.33	0.47
18	421	21.2	52.4	26.0	34.9	22.7	1.01	1.01
19	1025	28.6	78.7	26.3	34.8	22.2	0.96	1.21
20	1425	21.8	51.7	21.6	22.2	15.9	0.78	2.24
21	1734	19.9	91.3	13.9	17.4	12.2	1.07	0.99
22	1250	32.9	62.2	25.4	33.1	19.8	1.09	0.86
23	1008	21.6	43.1	21.5	25.7	19.0	1.28	0.78
24	867	30.1	43.3	21.8	23.0	19.0	1.10	1.00
25	1484	34.1	65.0	23.7	26.3	17.8	1.14	0.88
26	607	18.2	44.3	22.8	30.8	18.7	1.01	1.05
27	692	15.5	45.0	17.6	26.1	16.3	0.85	1.86
28	669	24.3	88.1	24.5	28.8	20.9	0.91	1.60
29	944	30.1	40.4	20.6	27.2	18.5	1.06	0.79
30	444	25.7	101.0	27.7	36.0	24.8	0.92	1.48
31	1117	36.6	65.7	29.4	33.7	24.0	1.31	0.56
32	857	20.4	55.9	21.1	23.7	17.8	1.27	0.70
33	500	37.5	94.9	28.1	37.5	26.8	1.08	0.67
34	1034	29.9	50.8	25.7	29.4	20.7	1.20	0.90
35	625	19.2	67.3	22.8	26.9	20.1	1.05	0.97
36	850	21.5	65.7	25.1	27.1	20.2	0.93	1.35
37	1667	34.8	58.5	19.8	21.6	15.3	1.03	1.01
38	1032	17.3	49.8	23.3	26.5	18.8	0.66	5.46
39	3750	41.4	13.7	11.1	13.1	9.6	1.79	0.21
40	1175	22.9	46.3	25.3	30.5	20.7	1.03	1.18
41	1934	24.1	42.4	20.0	20.7	15.0	1.05	0.65
42	1267	36.4	58.4	17.8	24.1	15.9	1.19	0.54
43	1475	17.7	68.3	19.4	18.4	14.0	0.94	1.45
44	3250	52.5	59.7	21.1	18.6	15.0	1.18	0.69
45	190	39.9	102.3	22.8	24.8	18.5	0.98	1.01
46	784	21.1	57.5	25.2	30.2	20.2	1.04	0.78
47	2050	41.7	24.7	16.6	19.3	13.5	1.59	0.27
48	2933	32.6	16.9	13.5	13.5	10.9	1.57	0.33
49	1766	36.4	64.1	23.7	24.7	17.5	0.91	1.17