

SILVA FENNICA



1987 · Vol. 21 N:o 1



SUOMEN METSÄTIETEELLINEN SEURA
SOCIETY OF FORESTRY IN FINLAND

PUBLISHER – JULKAISIJA

The Society of Forestry in Finland
Suomen Metsätieteellinen Seura r.y.

EDITORS – TOIMITUS

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A tentative model for describing the effects of some regenerative processes on the properties of natural seedling stands

Seppo Kellomäki, Heikki Hänninen, Taneli Kolström, Ahti Kotisaari & Timo Pukkala

TIIVISTELMÄ: ALUSTAVA MALLI SIEMENTYMISEN, TAIMIEN SYNNYN JA KASVUN VAIKUTUKSESTA LUONTAISEN TAIMIKON RAKENTEeseen

Kellomäki, S., Hänninen, H., Kolström, T., Kotisaari, A. & Pukkala, T. 1987. A tentative model for describing the effects of some regenerative processes on the properties of natural seedling stands. Tiivistelmä: Alustava malli siementymisen, taimien synnyn ja kasvun vaikutuksesta luontaisen taimikon rakenteeseen. Silva Fennica 21 (1): 1–10.

The effects of the size of seed crop, dispersal of seeds and the early development of seedlings on the density and spatial distribution of young Scots pine (*Pinus sylvestris* L.) stands are evaluated on the basis of theoretical models. The models include (i) the number and spatial distribution of parent trees on the regeneration area, (ii) the size of the annual seed crop, (iii) the seed dispersal from a particular parent tree, (iv) the germination of the seeds (germination percentage), (v) the death of aging seedlings after the establishment process and (vi) the height growth of the seedlings.

As one would expect the stand density and spatial distribution varied within a large range in relation to the density of the parent trees and the distance from them. The simulations also showed that natural seedling stands can be expected to be heterogenous due to the geometry of seed dispersal, emphasizing the frequency of young and small trees. The properties of the seedling stands were, however, greatly dependent on the density of the parent trees and the length of the regeneration period.

Tutkimuksessa on teoreettisesti tarkasteltu siemensadon suuruuden ja siementen leviämisen sekä siementen itämisen ja taimien ensikehityksen vaikutusta syntyvän taimikon tiheyteen ja taimien ikä- ja kokojakaumiin. Näiden perusteella laadittiin luontaista uudistumista kuvaava simulointimalli. Tehdyt laskelmat osoittivat luontaisesti syntyneen taimikon olevan aina tiheydeltään vaihtelevan sekä edustavan iältään ja kooltaan vinoja jakaumia, joissa nuorien ja kooltaan pienien taimien osuus on suuri. Taimikoiden ominaisuudet riippuivat kuitenkin suuresti siemenpuuston tiheydestä ja uudistumisajan pituudesta.

Key words: *Pinus sylvestris*, model, natural regeneration, seed dispersal, parent tree, Scots pine
ODC 231+181.52+174.7 *Pinus sylvestris*+236.4

Correspondence: Seppo Kellomäki, University of Joensuu, Faculty of Forestry, P.O. Box 111, SF-80101 Joensuu, Finland.

Approved on 23. 1. 1987

1. Introduction

The success of natural regeneration is closely related to the regenerative biology of forest trees and the prevailing soil and climatic conditions. For example, size of seed crop, dispersal of seeds, germination of seeds and growth of germinants affect the density of the seedling stand and the distribution of seedlings in space. These processes are mainly controlled by soil and climatic factors, especially temperature and moisture conditions. Consequently, the varying distributions of size and age characteristic to natural seedling stands are also affected by the same factors (Harper 1977, Kotisaari 1982).

The concepts of seed crop, seed dispersal, germination of seeds and growth of germinants are widely used in describing the regenerative process of forest trees and the factors controlling it (e.g. Yli-Vakkuri 1961). Each phase succeeds the previous one in such a way that the embryos representing the seed crop of a particular year and the resulting seedlings can be treated as a separate cohort. Thus, each cohort of seedlings are due to a process where the cohort of embryos will experience the sub-processes of formation of seed crop, dispersal of seeds, germination of seeds and growth of germinants (Hett 1971, Harper 1977).

The members of any natural seedling stand are recruited by repeated seed crops which contribute a varying number of seedlings into the stand (cf. Lehto 1956, 1969, Hett 1971, Hänninen et al. 1972, Hett & Loucks 1976, Kinnunen & Mäki-Kojola 1980). Therefore any natural seedling stand seems to be a product of the accumulation of seedlings representing successive seed crops during a prolonged period (Hänninen et al. 1970). This process will produce a stand representing a varying age and size distribution of seedlings

with an irregular location in space. Therefore one can expect that any natural seedling stand is characterised by varying age and size distribution associated with an irregular location of seedlings in space (Lehto 1956, Yli-Vakkuri 1961, Hänninen et al. 1970, Pohtila 1980).

This study attempts to demonstrate principles how the regenerative process affects the properties of natural seedling stand. In particular, the role of density of parent trees, dispersal of seeds, germination of seeds and growth of germinants are evaluated regarding the density and age and size distribution of the resulting seedling stand. The following limitations of the study are of importance in evaluating the results:

(i) The study is theoretical, the main emphasis being on developing a tentative model for predicting the seed crop, seed dispersal onto a particular place, establishment and growth of seedlings and the consequent structure (density and age and size distributions) of the seedling stand after a particular time elapsed from the regenerative cutting.

(ii) The effects of environmental factors like temperature, soil moisture and others on the control of the regenerative processes are deliberately excluded in order to recognize the role of the selected processes in establishing the structure of a seedling stand.

The results of the model construction are demonstrated based on simulations representing selected conditions for the regeneration.

The authors acknowledge the constructive support expressed towards this study by Prof. Matti Leikola (University of Helsinki), acting Prof. Pentti K. Räsänen (University of Helsinki) and Dr. Heikki Smolander (Finnish Forest Research Institute).

2. A model for the natural regeneration of forest trees

Outlines of the model. The model for the natural regeneration of forest trees incorporates four sub-models which describe the respective sub-processes of the regenerative process of a seedling stand (Fig. 1).

- (i) A model for the size of seed crop.
- (ii) A model for seed dispersal.
- (iii) A model for the germination seeds and the survival of germinants.
- (iv) A model for the growth of the germinants.

The input of the model includes the properties of the stand of the parent trees and site fertility. The properties of the parent trees are described by the density and location in the regeneration area, which determine the seeding geometry of the parent trees. Site fertility controls the establishment process of the seedlings. Thus, the seeding geometry and the establishment of the seedlings together determine the final output of the model, i.e. the seedling stand at a given moment after regeneration cutting as described, for exam-

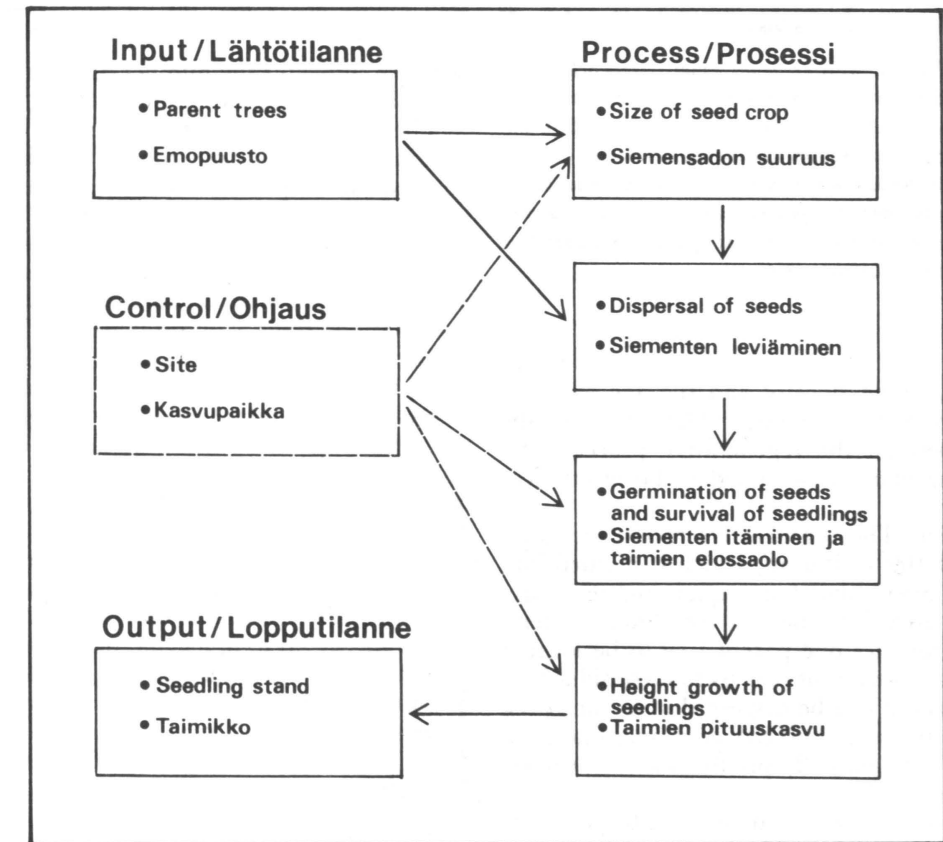


Fig. 1. Basic structure of the model for natural regeneration as compiled by the sub-processes of regeneration and the assumed effects of the sub-processes on the result of the regenerative process. The dotted line indicates the factors excluded in the construction of the model.

Kuva 1. Mallin rakenteen koostuminen uudistumistulokseen vaikuttavista osaprosesseista sekä osaprosessien oletetut vaikutussuhteet. Katkoviivalla on ilmaistu tekijöitä, joita ei ole sisällytetty kehitettyyn malliin.

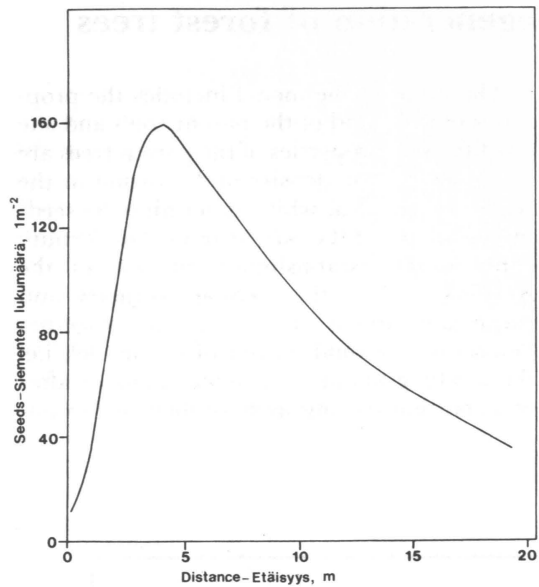


Fig. 2. The number of seeds per square metre originating from a particular parent tree as a function of the distance between the parent tree and a particular sample plot (Guittet & Laberche 1974).

Kuva 2. Yhden neliömetrin alalle yhdestä siemenpuusta tulevien siementen määrän riippuvuus tarkasteltavan alan ja puun välisestä etäisyydestä siemensadon ollessa maksimaalinen (Guittet & Laberche 1974).

ple, by stand density and the age and size pattern of the seedlings. The effects of the processes on the regenerative process of a seedling stand is assumed to be multiplicative.

Seeding. The regenerative model treats an area of $100 \times 100 \text{ m}^2$, which is divided into 10 000 area units of one square metre in size. These area units form a coordinate system, which facilitates one parent tree to be located onto each area unit. Let us first consider how many seeds can be dispersed onto each area unit from any parent tree assuming that each parent tree annually produces seeds at maximum capacity.

One can expect that the number of seeds dispersed onto a particular area unit from a particular parent tree is inversely related to the distance between the area unit and the parent tree (cf. Cremer 1966). We described this relationship with the help of equation (1) assuming a logistic decrease in seed number

as a function of the distance between the area unit and the parent tree (Fig. 2)

$$(1) S_i = 312.01 \left(\frac{1}{1 + e^{-1.29(M_i - 2.19)}} \right) e^{-0.16M_i}$$

where S_i is the number of seeds dispersed onto a particular area unit from the parent tree i and M_i the distance between the area unit and the parent tree. The parameters of the equation (1) are estimated on the basis of the empirical material presented by Guittet and Laberche (1974) for the dispersal of seeds from solitary Scots pines (*Pinus sylvestris* L.). The total number of seeds (S) dispersed onto any area unit is obtained as a sum of seeds dispersed from each parent tree in the regeneration area, i.e.

$$(2) S = \sum_{i=1}^n S_i$$

where n indicates the number of parent trees in a particular regeneration area.

The above consideration is based on the assumption that the annual seed crop is equal to maximum capacity. For example, just after

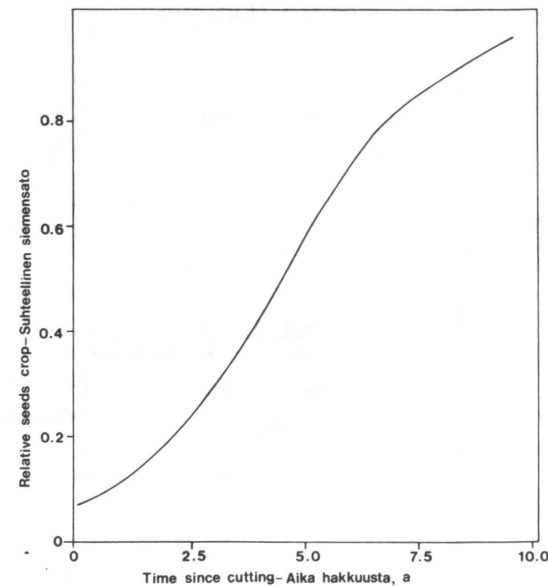


Fig. 3. The size of the seed crop as a function of the time since the regenerative cutting.

Kuva 3. Siemensadon suuruutta kuvaavan tasoparametrimin oletettu riippuvuus ajasta siemenpuuhakkuun jälkeen.

a regenerative cutting this assumption is not valid since several years are needed to obtain the maximum capacity of seed crop (e.g. Bergman 1980). Therefore we assumed that the seed crop will increase up to ten years after the regenerative cutting.

Let ST be a parameter indicating the capacity of the seed crop having values $(0 \dots 1)$. It is further assumed that the values of the parameter ST are related to the time elapsing after the regenerative cutting according to the logistic pattern indicated by the equation (3) (Fig. 3)

$$(3) ST_v = \frac{1}{1 + e^{-0.6v}}$$

where v is the specific year following the regenerative cutting and ST_v the value of the parameter ST in the year v . Assuming that the effect of the parameter ST on the size of the seed crop is multiplicative one can obtain the values of the seed crop in the years v (S_v) through equations (2) and (3) as follows

$$(4) S_v = ST_v \cdot S$$

Establishment of seedlings. It is well-known that only a small fraction of the total number of seeds dispersed on a particular area unit in a given year will produce surviving seedlings (e.g. Yli-Vakkuri 1961, Yli-Vakkuri & Räsänen 1971). We assumed this fraction to be one percent of the seed number representing a given cohort as argued by Guittet & Laberche (1974) regarding the success of establishment of seedlings in the ground vegetation.

Thereafter the survival of the germinants is assumed to follow the dependence given in Fig. 4 as a function of the age of the cohort. At the same time the height of the germinants is assumed to increase as given in Fig. 5. The function for the height growth is estimated on the basis of the results by Skoklefeld (1965), Bergan (1981) and Saksa (1983).

Computations. The above model has been transformed into a computer algorithm written in Fortran77. In the algorithm the regenerative period (total time elapsing from the regenerative cutting to the removal of the parent trees) is selective with a time step of one year. In any model run the following computations are carried out for each year.

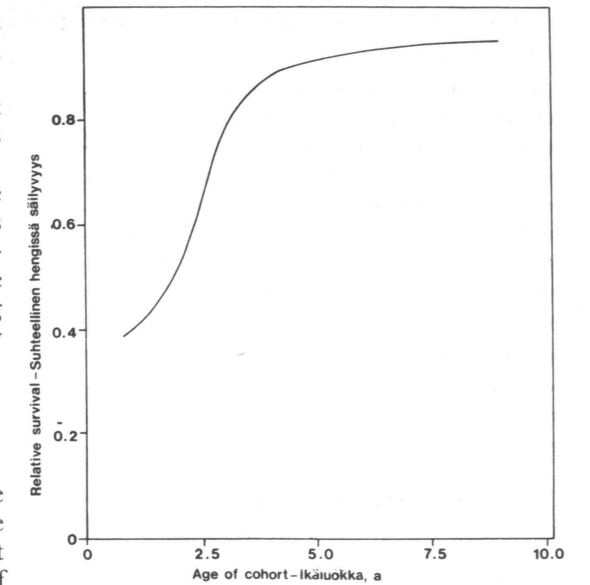


Fig. 4. The percentage of living seedlings as a function of the age of the seedling cohort (Guittet & Laberche 1974).

Kuva 4. Taimen elossäsäilyvyyden riippuvuus iästä, tarkastelujaksoneksi yksi vuosi. Kuvan riippuvuus määritetty Guittet'in ja Laberche:n (1974, s. 126) mäntyä koskevien empiiristen tulosten perusteella.

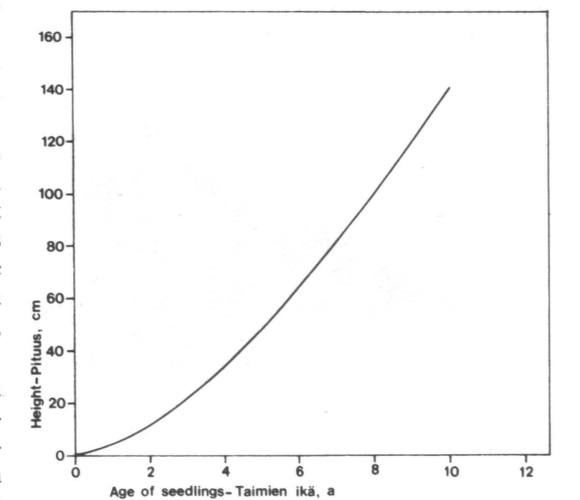


Fig. 5. The height of *Pinus sylvestris* seedlings as a function of the age.

Kuva 5. Männyn taimien pituuden riippuvuus iästä.

(i) Computation of the value of the parameter ST_v (equation 3).

(ii) Computation of the maximum number of seeds (S_i) dispersed from each parent tree onto a particular area unit (equation 1). Thereafter the realised number of seeds in each area unit is computed with the help of equation (4). Further, the number of the produced germinants ($0.01 \cdot S_v$) is calculated with the help of the number of seeds. The above computations are carried out separately for the each area unit of the regeneration area.

(iii) The number of seedlings in cohorts of the preceding years are reduced as depicted in Fig. 4. These computations are carried out separately for each area unit of the regeneration area.

After this has been done the following calculations are carried out in order to charac-

terize the seedling stand produced in the period following the regenerative cutting.

(i) The number of living seedlings in each cohort are counted applying a time step of one year.

(ii) The height distribution of the seedlings is computed applying a height interval of five centimetres.

(iii) The number of living seedlings on each area unit (stand density) is computed in terms of seedlings per hectare.

The results of the computations can be obtained in the form of numbers or figures depending on the preferences of the algorithm's user.

3. Examples of the results of the simulations

3.1. Density of the stand

In the following are some examples demonstrating the structure of the seedling stand at varying input of the model. For example, the density of the seedling stand is the greatest just outside the crown projection of the parent tree decreasing towards and outwards of the parent tree (Fig. 6). This pattern is repe-

ated around each parent tree. In a widely spaced stand of parent trees this results in a great variability in the density of seedling stand. In a narrowly spaced stand of parent trees the variability in the density of the seedling stand diminishes (Fig. 7). In this case the only exception is in the closest surroundings of the parent trees, where there are only few seedlings per area unit.

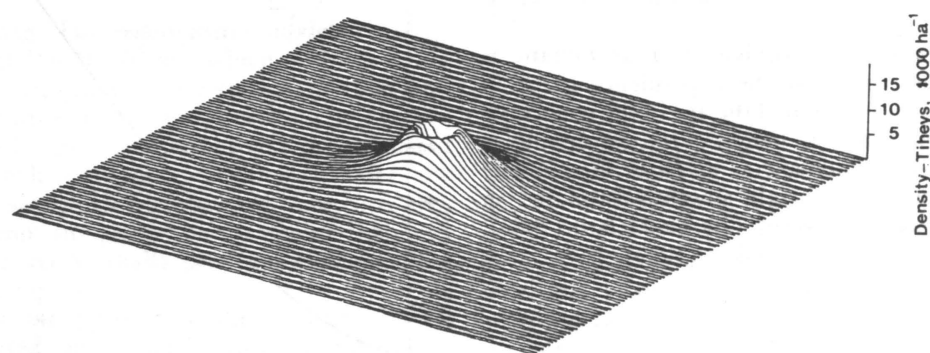


Fig. 6. Variability of the density of the seedlings around parent tree eight years after the regenerative cutting. The area of the figure is 100×100 m and the maximum density of the seedling stand 13381 seedlings/ha.

Kuva 6. Taimikon tiheyden vaihtelu yksittäisen puun ympärillä kahdeksan vuotta uudistamishakkuun jälkeen. Kuva-ala on 100×100 m ja taimikon maksimitiheys 13381 tainta/ha.

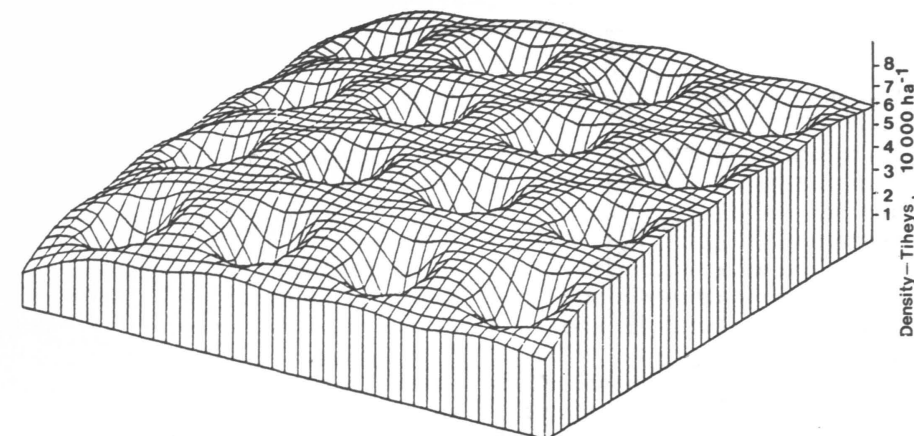


Fig. 7. Number of seedlings on the regeneration area eight years after the regenerative cutting. The density of the parent trees is 100 stems per hectare. Spatial distribution of the parent trees is homogenous. The area of the figure is 40×40 m and the maximum density of the seedling stand 64974 seedlings/ha.

Kuva 7. Taimikon tiheyden vaihtelu uudistuslalla kahdeksan vuotta uudistushakkuun jälkeen, kun emopuuston tiheys on 100 runkoa/ha ja puiden tilajakauma tasainen. Kuva-ala on 40×40 m ja taimikon maksimitiheys 64974 tainta/ha.

3.2. Accumulation of seedlings and the properties of the seedling stand

The density of the seedling stand at a given moment is the result of the accumulation of seedlings prior to that moment. The total accumulation of seedlings (density of the seedling stand) depends on the length of the regenerative period (the length of time since the regenerative cutting) and the density of the parent trees (Fig. 10). Obviously, a particular density of a seedling stand can be obtained in a shorter time in a densely-spaced stand of parent trees than in a widely-spaced stand.

The accumulation of seedlings in the early part of the regeneration period ($v < 10a$) is nearly linearly related to time and the density of the parent trees. Later, the total number of seedlings will decrease and level off at the level where the birth and death rates of the seedlings are balanced. Seedling stands at a given moment following the regeneration cutting are representative of stand structure where the number of young and small seedlings dominates, i.e. the size and age distributions are skewed to the right (Figs. 8 and 9).

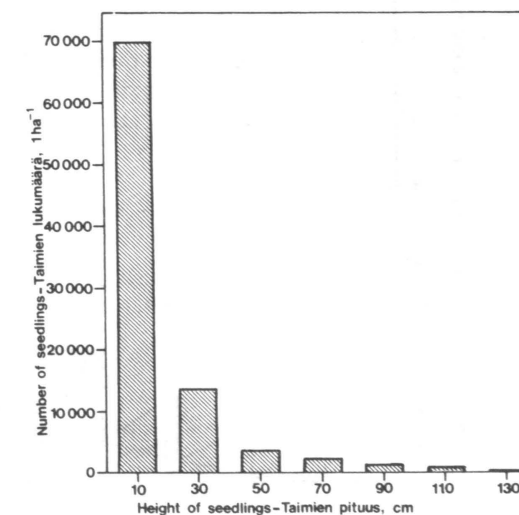


Fig. 8. Height distribution of seedlings eight years after the regenerative cutting. The density of the parent tree stand is 100 stems/ha.

Kuva 8. Taimien pituusjakauma uudistuslalla kahdeksan vuotta uudistushakkuun jälkeen. Emopuuston tiheys 100 runkoa/ha.

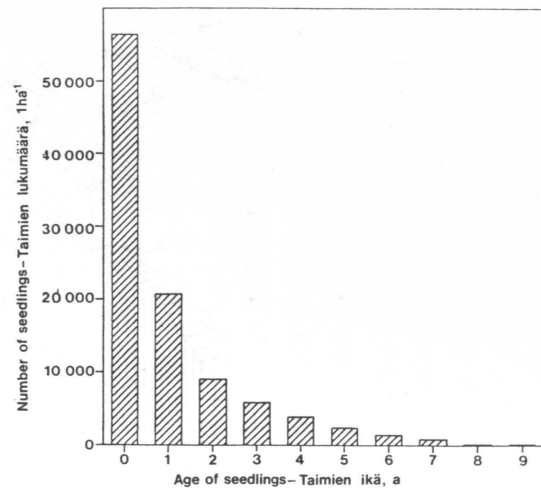


Fig. 9. Age distribution of seedlings eight years after the regenerative cutting. Density of the parent tree stand is 100 stems/ha.

Kuva 9. Taimien ikäjakauma uudistuslalla kahdeksan vuotta uudistushakkuun jälkeen. Emopuuston tiheys on 100 runkoa/ha.

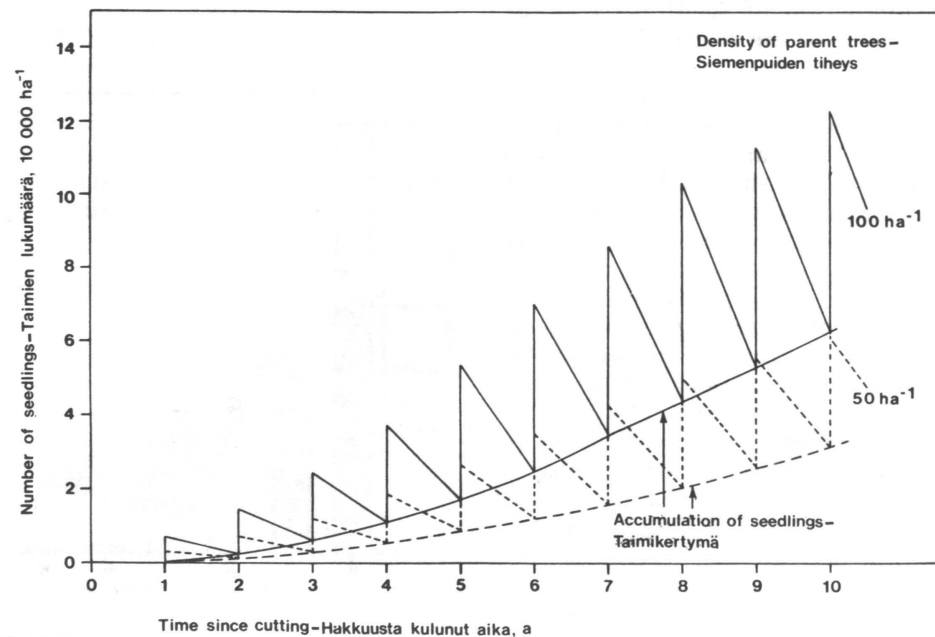


Fig 10. The cumulative number of seedlings in the regeneration area during the eight years since the regenerative cutting. The density of the parent tree stand is 50 and 100 trees/ha.

Kuva 10. Taimien kokonaiskertymä uudistuslalle kahdeksan vuoden aikana uudistushakkuusta. Emopuuston tiheys 50 ja 100 runkoa/ha.

4. Discussion

The main emphasis in this study is to demonstrate how the seeding and establishment of seedlings affect the structure of the seedling stand. The model calculations demonstrate that the seeding geometry (density of parent trees, dispersal of seeds) results in a pronounced variation in the spatial distribution of seedlings. This variation is further emphasized by the establishment of germinants, i.e. only few seedlings from each seed crop will be recruited into the stand. Consequently, any natural seedling stand can be expected to represent age and size distributions skewed to the right, i.e. dominance of small seedlings in the total number of seedlings accumulated through the given moment since the regenerative cutting.

The present model for the natural regeneration of forest trees is still a tentative one, the emphasis on factors most probably having the pronounced effect on the structure of the seedling stand. We believe, however, that the model will already be useful for anybody willing to evaluate, for example, the probable effects of the seeding geometry on the structure of the seedling stand. This is important, if the influence of weather and the soil properties on the structure of the seedling stand are to be recognised.

The model computations, however, yield seedling stands which have a structure resembling the real one, i.e. variable location of

seedlings representing variable age and size distribution (e.g. Lehto 1956, Pohtila 1980). This is, however, no indicator of the reliability of the model, but each sub-model should be verified separately on the basis of the material describing this particular process. This kind of elaboration is also necessary for further development of the model, to make it responsive to factors other than those assumed in this study to be effective regarding the regeneration process.

The structure of the model facilitates its easy expansion to cover more factors affecting the results of the regeneration. For example, the role of prevailing wind conditions should be incorporated into the model, since it modifies the seeding geometry, depending, for example, on the rate and turbulence of the air flow. Obviously, the treatment of the seed crop is also too simple, since only the trend-like increase of the seed crop after the regenerative cutting is included in the model. For instance, the variation in seed crop due to weather patterns and the ontogeny of the parent trees should be incorporated into the model in order to make it more realistic (Pukkala 1985). Similarly, the influence of the germination and growth conditions (e.g. soil moisture and temperature) is to be introduced into the model in a more detailed form than is presently the case.

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