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Growth and yield models for uneven-sized forest stands in Finland

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ABSTRACT

Uneven-sized forestry is gradually gaining popularity and acceptability also in the Nordic countries. This is because of the willingness of the public and some forest owners to avoid clear-fellings and pursue more near-nature forest structures. It has also been realized that the profitability of uneven-sized forestry may be competitive with even-aged forestry. In Finland, management of uneven-sized stands is hampered by the lack of information about the dynamics of such stands, and about the yield and profitability of uneven-sized forestry. This study developed models which allow managers to simulate the growth and yield of uneven-sized stands in Finland, making it possible to predict the yield and analyze the sustainability of different management options. The model set consists of individual-tree diameter increment, height and survival models, and a model for ingrowth. The modeling data consisted of two long-term field experiments of uneven-sized forest management, a set of temporary sample plots measured earlier for growth modeling purposes, and the sample plots of the third National Forest Inventory of Finland. The application area of the models covers all growing sites, all main tree species, and the whole surface area of Finland. According to the models, the sustainable harvest of a fertile (Oxalis-Myrtillus site) uneven-sized Norway spruce forest varies between 5.5 and 7 m³ ha⁻¹ a⁻¹ in Central Finland, depending on the length of the cutting cycle, stand density, and shape of the diameter distribution. It is profitable to harvest large diameter classes more heavily than small ones. Due to the large amount of data the models for diameter increment are highly significant and reliably show the growth level of trees in uneven-sized stands. The weakest models are the ingrowth models, which are based on a clearly smaller data set than the other models.

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1. Introduction

The main silvicultural aspects in raising uneven-aged and uneven-sized stands are the range and shape of stem frequency distribution, together with stand volume or basal area. The term uneven-aged is commonly used although knowledge on tree ages is often lacking. It has been assumed that size differences represent differences in age (Daniel et al., 1979). However, trees grown in the open differ considerably in size from understory trees of the same age. Understory trees, once released, may reach the same size as trees grown in the open but at a clearly older age (Tarasink and Zwiernirski, 1990). In fact, the abundance of understory trees and their capacity to tolerate shade and recover are of vital importance in uneven-sized management.

The shape of the diameter distribution of uneven-sized and uneven-aged forest is often a reversed J-curve. This kind of distribution is commonly characterized by the q coefficient (also called q ratio), which is the ratio between tree frequencies in two adjacent diameter classes. The q ratio is often considered constant through the whole distribution, ranging from 1.2 to 2.0 between adjacent 4-cm-wide diameter classes, but it may also vary within the range of diameters (Cancino and Gadow, 2002). A high q coefficient would mean that small trees occupy much growing space although they do not produce much economic return (O'Hara, 1996). Therefore, a low q ratio, at least within small diameter classes, may lead to better economic results by yielding a higher number of large trees. The distribution may also resemble a rotated sigmoid (Goff and West, 1975; Schütz, 1989) or bi-modal curve (Westphal et al., 2006).

The old national forest inventories of Finland and Sweden indicate that the forests in the Boreal Zone of Europe have mainly consisted of uneven-sized mixed stands (Nilsson and Östlin, 1961; Lähde et al., 1991, 1999). Other studies, based on experimental areas, support these findings (Huse, 1965; Hytteborn et al., 1987). Stands with a reverse J-shaped diameter distribution have been the most prevalent (Lähde et al., 1991, 1999; Zackrisson et al., 1995). This kind of stand structure seems to have been a result of natural

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disturbances and dynamics of boreal forests. However, the reverse J-shaped curve is not the only applicable model for describing virgin uneven-sized forests (Westphal et al., 2006).

Comparison of alternative management options of forest stands requires long-term field experiments, permanent inventory plots or a set of models that can be used to predict the consequences of management alternatives. Since the field experiments of unevensized or -aged forestry in Finland have been very few and only recent, modeling is the most useful means to provide comprehensive management support in the near future (Cancino and Gadow, 2002). In the Nordic countries, very few growth models have been presented for uneven-sized management (Pukkala and Kolström, 1988; Lähde, 1992b; Lähde et al., 1999; Eerikäinen et al., 2007). However, there is plenty of experience elsewhere in modeling the dynamics of uneven-sized stands (e.g., Vanclay, 1994; Peng, 2000; Porté and Bartelink, 2002; Trasobares and Pukkala, 2004; Trasobares et al., 2004; Palahí et al., 2008). Groot et al. (2004) suggest that individual-tree models may be the most suitable approach to modeling the dynamics of uneven-sized stands. According to Vanclay (1994), the required model set in this approach consists of diameter increment, mortality and recruitment models.

Although uneven-sized and multi-layer stands commonly exist in Finland, uneven-sized forestry is currently rare. Due to changes in forest usage and demands by the public for more near-nature forest management and greater forest diversity (Lähde et al., 1999), development of models for uneven-sized forestry has become more and more urgent. This study aimed at filling that obvious gap in forestry models in Finland. It developed the first complete set of growth and yield models that are specifically targeted for simulating the development of uneven-sized forests in Finland.

2. Material and methods

2.1. The required model set

Prediction of forest development may use stand-level or treelevel models. In Finland, individual-tree models have been used in even-sized management already for three decades since they allow a more detailed stand description and are flexible in terms of analyzing stand development after different types of cuttings (e.g., Hynynen et al., 2002). In uneven-sized forestry, the following set of models is required in the individual-tree approach (e.g., Vanclay, 1994; Trasobares et al., 2004):

- Individual-tree diameter increment model.
- Individual-tree survival model.
- Individual-tree height model or height increment model.
- Ingrowth model.
- Model for the diameter of ingrowth trees.

This study developed the above-mentioned model set. A static height model was developed instead of height increment model because of the lack of height increment data. A 5-year time step was used in the modeling of diameter increment and ingrowth.

2.2. Materials

The following materials were used in modeling (Tables 1 and 2):

- Field experiments of uneven-sized forest management in Vessari and Honka (referred to as Vessari-Honka data); 17,070 observations; 104 plots with 1–3 six-year measurement intervals per plot.
- A set of pine and spruce plots in the southern part of North Karelia (Karelia data); 11,792 observations; 158 plots.
- Plots of the third National Forest Inventory (NFI3 data); 23,290 observations; 2040 plots.

Table 1

Characteristics of the data set used in diameter increment modeling.

	Minimum	Mean	Maximum
Pine (15,282 observations)			
Number of trees per hectare	90	1430	9720
Stand basal area (m ² ha ⁻¹)	0.3	15.0	50.0
Mean diameter (cm)	4.2	17.0	38.3
Tree diameter (cm)	2.0	16.2	52.8
Basal area of larger trees $(m^2 ha^{-1})$	0.0	8.3	46.6
Spruce (24,014 observations)			
Number of trees per hectare	130	1804	9720
Stand basal area $(m^2 ha^{-1})$	1.9	21.2	50.0
Mean diameter (cm)	4.2	17.8	38.3
Tree diameter (cm)	2.0	12.7	96.6
Basal area of larger trees (m ² ha ⁻¹)	0.0	15.5	51.3
Birch (8219 observations)			
Number of trees per hectare	140	1900	9600
Stand basal area (m ² ha ⁻¹)	1.8	17.5	50.0
Mean diameter (cm)	4.2	16.3	34.1
Tree diameter (cm)	2.0	14.0	51.4
Basal area of larger trees (m ² ha ⁻¹)	0.0	11.0	49.3

A sub-set of this data was used in height modeling and survival modeling.

These data sets were used for different models as follows:

- Diameter increment models: all data sets.
- *Height models*: Vessari-Honka (height measurements of 2002) and NFI3.
- Ingrowth models: Vessari-Honka and Karelia.
- Models for the diameter of ingrowth: Vessari-Honka and Karelia.
- Survival models: Vessari-Honka.

2.3. Vessari-Honka data

The Vessari and Honka field experiments were established in Central Finland, Vessari on a herb-rich (Oxalis-Myrtillus type) and Honka on mesic (Myrtillus type) mineral soil site. In South and Central Finland, the most common forest site types on mineral soils are Oxalis-Myrtillus (OMT), Myrtillus (MT), Vaccinium (VT) and Calluna (CT), which approximately correspond to the following Scots pine site indices (dominant height at 100 years): OMT, 30 m; MT, 27 m; VT, 24 m; CT, 18 m (for more information on site types, see Cajander, 1949). The original stands of the experiments were dominated by Norway spruce (Picea abies L. Karsten) with a mixture of Scots pine (Pinus sylvestris L.), birch (Betula pendula Roth. and B. pubescens Ehrh.), and some other broadleaves. Shelterwood cuttings were carried out in the late 1940s but there were already understory trees in the stands born before the regeneration fellings. The seed trees were felled in Honka in 1957 and in Vessari in 1961, once regeneration was well under way. After that, the stands were divided into square plots (50 m \times 50 m in Vessari and 40 m \times 40 m in Honka). The plots were thinned and cleared mechanically by liberating dominant conifer saplings from competitors and co-dominants. After that, regeneration of broadleaves and Norway spruce trees continued from the adjoining stands, and understory trees recovered gradually.

Table	2
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Characteristics of the data set used in ingrowth modeling (371 observations).

	Minimum	Mean	Maximum
Number of trees per hectare	120	1937	8467
Stand basal area (m ² ha ⁻¹)	0.3	22.5	52.5
Mean diameter (cm)	5.6	18.2	38.3
Pine ingrowth (trees ha ⁻¹)	0.0	43.9	1533.3
Spruce ingrowth (trees ha ⁻¹)	0.0	45.8	544.4

In order to eliminate the edge effect caused by different treatments, and to ease monitoring, a circular plot of 0.03 ha was established in the middle of each square plot. The first thinning was done in Vessari in winter 1986 and in Honka in winter 1987, the second thinning in spring 1994, the third one in 2002, and the fourth one in 2008. After the thinnings, stand density and tree species composition varied a lot between the plots. Monitoring measurements on the mapped 0.03 ha plots were started before the second thinning in spring 1994, and were thereafter repeated at three-year intervals until 2008.

The following six-year periods were used as observations in Vessari-Honka data: 1994–1999, 1997–2002 and 2000–2005. The six-year diameter increments of each tree were obtained as the difference between two corresponding diameter measurements. The increments were converted into five-year increments by multiplying by 5/6. Only those plots were used for modeling which were not thinned during the six-year period. Characteristic to the Vessari-Honka data set was a small number of pine and birch trees, lack of site variation, a rather small number of large trees, and lack of mixed stands. The greatest advantage of the data set was that the plots represented truly uneven-sized structures and treatments.

2.4. Karelia data

The Karelia data set was used to obtain more pine observations, dense stands, large trees, and mixed stands. This data consisted of 158 plots, out of which 66 were pure or almost pure pine stands, 49 pure or almost pure spruce stands, and 43 pine-spruce mixtures. The plots had been measured for developing distancedependent growth models for mixed and pure pine and spruce stands (e.g., Pukkala et al., 1998; Pukkala and Miina, 1998; Miina and Pukkala, 2000). The plots were selected so as to have large variation in the competitive status of trees both within and between the plots. Therefore, the plots included heterogeneous stand structures with large variation in tree size, degree of mixture, and spatial distribution of trees. Few of these plots represented strictly uneven-sized stands but the data set included plenty of individual trees with similar competitive situation as trees growing in uneven-sized stands. Most of these plots were on Myrtillus type, but some spruce-dominated plots were on Oxalis-Myrtillus type, and a few pine-dominated plots on Vaccinium type (sub-xeric site). In the Karelia data set the diameter increment of one 5-year period was known for every tree exceeding 3 cm dbh. The data set was used for diameter increment and ingrowth modeling.

2.5. NFI3 data

Plots of the third National Forest Inventory (NFI3), carried out in 1951–1953, were used as additional data source to have more pine and birch observations, more large and old trees, and more geographical and site variations. The reason for using that old data was the fact that until 1950 forests had been treated mainly by selection cuttings and most stands were uneven-sized, i.e., naturally regenerated and understory trees not cleared (Lähde et al., 1991, 1999). Concentric circular plots, 0.1 ha for trees larger than 10 cm in dbh and 0.01 ha for trees 2–10 cm in dbh, had been used in the inventory. Each plot had been placed entirely within one stand. Thus, the stand structure within a plot could not have been an admixture of different stands. The plots, 15,310 in number, had been measured at intervals of 1 km along the inventory lines (Ilvessalo, 1951). Radial increment of the past five years and height had been measured from sample trees.

Only a sample of the NFI plots was selected for modeling (2040 plots). This was because the NFI data had some drawbacks

that make them a less valuable data source than the two other sets. The main shortcoming was that the past growth had been measured from sample trees only, which means that projecting the stand conditions 5-years back, to the beginning of the prediction period, was less reliable than in the other data sets. In addition, only sample trees were known individually; the other growing stock was described by the number of trees in 4-cmwide diameter classes. Due to these reasons, calculation of the model predictors was less accurate in NFI3 data than in the other data sets.

NFI plots were selected to modeling data with a probability of 0.1 with the following exceptions:

- the probability was 0.6 if there were trees larger than 36 cm within the plot,
- otherwise the probability was 0.3 if there were trees larger than 32 cm,
- otherwise the probability was 0.2 if there were trees larger than 28 cm,
- if the stand had been treated with selection felling (according to the recordings) the probability was 0.4,
- if the stand had been classified as over-aged the probability was 0.2,
- if the age of dominant trees was more than 100 years the probability was 0.2,
- if the site was not of medium fertility (*Myrtillus* type) the probability was 0.2,
- if the site was more fertile than *Oxalis-Myrtillus* type or poorer than *Vaccinium* type the probability was 0.4, and
- if the site was poorer than Calluna type the probability was 0.6.

These rules resulted in more than one probability for a plot. The highest probability was used in the selection. A randomly selected plot was accepted only if it had at least eight growth sample trees. The sample trees were used to make a plot-specific past growth model. This model was used to predict the diameters of trees 5 years earlier, i.e., in the beginning of the 5-year period. The past growth model was linear with dbh as the only predictor. The sample trees, which were also measured for height, were used as observations in diameter increment modeling and height modeling.

2.6. Modeling

The potential predictors of the diameter increment model described the following factors:

- Tree size: dbh (cm),
- *Competition*: stand basal area and basal area in larger trees (*BAL*, m² ha⁻¹) and its modification such as ln(*BAL*), *BAL*/ln(*dbh*+1), *BAL*/G, 1–*BAL*/G (see e.g., Wykoff, 1990; Vanclay, 1994), and
- Site: forest site type and temperature sum (sum of degree days over 5 °C).

It is noteworthy that the age of trees and stands were not used as predictors since stand age is "undefined" for uneven-aged stands, and tree ages are seldom measured in the inventories of uneven-sized stands. Therefore, an assumption in modeling was that, in a give stand, a tree of certain size and facing a certain amount of competition always grows similarly regardless of its age. Due to the omission of age, site index based on age and dominant height was not used either. Such a combination of predictors and their transformations was pursued that the statistical significance of each predictor was high, the number of predictors was low, and the influence of each predictor was logical and corresponded to previous knowledge.

)

(2)

In height modeling, only such variables were used which describe tree size and site; variables that describe competition will change in cuttings, and may cause an instant change in the predicted height of a tree and therefore cause non-logical simulation results.

The survival model was a logistic model which guarantees that the predicted probability of survival will be between zero and one. Only the Vessari-Honka data set was used for the survival modeling, yielding two models: one for spruce and the other for pine and birch trees. Since the measurement interval of Vessari-Honka was six years, the models predict six-year survival, which must be taken into account when using the models.

The ingrowth limit was taken as 5 cm. Therefore, the ingrowth model predicts the number of such trees that will pass the 5-cm dbh limit during the following 5-year period. In Vessari-Honka, the measured 6-year ingrowth was converted into 5-year ingrowth by multiplying with 5/6. The model for the diameter of ingrowth predicts the mean diameter of the ingrowth trees at the end of the 5-year period. In the Vessari-Honka data set the measured mean diameter of ingrowth trees is for the end of a six-year period. Therefore, modeled one-year growth of small trees (typically around 0.05 cm) was subtracted from the diameter to obtain an estimate for the mean diameter of ingrowth trees at the end of a 5-year period.

3. Results

3.1. Diameter increment model

The model for the 5-year diameter increment was of the following form:

$$\ln(i_{d}) = a_{1} + a_{2}BAL_{\text{Spruce}} + a_{3}BAL_{\text{Other}} + a_{4}\ln(G) + a5\sqrt{d} + a_{6}d^{2} + a_{7}MT + a_{8}VT + a_{9}CT + a_{10}ClT + a_{11}\ln(TS)$$
(1)

where i_d is the 5-year over-bark diameter increment (cm), *d* is the diameter at breast height (cm), *G* is the total basal area of trees larger than 5 cm in dbh (m² ha⁻¹) and *TS* is the temperature sum (degree days). *MT*, *VT*, *CT* and *ClT* are indicator variables which indicate whether the site type is *Myrtillus* (*MT*), *Vaccinium* (*VT*), *Calluna* (*CT*) or *Cladonia* and poorer (*ClT*). In one stand, only one indicator variables are zeroes, the model predicts the growth on *Oxalis-Myrtillus* type. *BAL* is the basal area of trees larger than the subject tree (m² ha⁻¹), which was computed separately for spruce (*BAL*_{Spruce}) and other tree species (*BAL*_{Other}). *BAL* describes the competitive position of a tree within a stand. It was the strongest individual predictor. Due to the high number of observations, all predictors of all models were very significant, their *t* values ranging from 8 to 60.

Due to the logarithmic transformation of the predicted variable, the Snowdon correction factor (Snowdon, 1991) was calculated for the models (Table 3). The corrected growth prediction is obtained from:

$$i_{d,corrected} = Correction factor \times exp(ln(i_d))$$

where $ln(i_d)$ is the prediction of model 1.

The regression coefficients of the models for different tree species (Table 3) indicate, i.a., that trees grow better in mixed stands than in pure stands. In the model for spruce, *BAL*_{Spruce} has a more negative coefficient than *BAL*_{Other} indicating that a spruce competitor reduces the growth of a spruce more than another species of the same size. Increase in stand basal area, or in basal area of larger trees, decreases diameter increment whereas increasing tree size first improves growth and then begins to

Table 3

Parameters of the diameter increment models (Eq. (1)).

Pine	Spruce	Birch
-7.758	-5.317	-11.873
-0.0530	-0.0106	-0.0304
-0.0335	-0.0430	-0.0474
-0.266	-0.486	-0.173
0.237	0.455	0.446
-0.000901	-0.000927	-0.00123
-0.238	-0.180	-0.121
-0.333	-0.450	-0.227
-0.612	-0.929	-0.524
-1.201	-	-
1.229	0.823	1.627
15,282	24,014	8,219
0.400	0.568	0.541
0.527	0.604	0.599
1.110	1.124	1.127
	Pine -7.758 -0.0530 -0.0335 -0.266 0.237 -0.000901 -0.238 -0.333 -0.612 -1.201 1.229 15,282 0.400 0.527 1.110	Pine Spruce -7.758 -5.317 -0.0530 -0.0106 -0.0335 -0.0430 -0.266 -0.486 0.237 0.455 -0.000901 -0.000927 -0.238 -0.180 -0.333 -0.450 -0.612 -0.929 -1.201 - 1.229 0.823 15,282 24,014 0.400 0.568 0.527 0.604 1.110 1.124

The predicted variable is the logarithm of 5-year diameter increment.

reduce it (Figs. 1 and 2). The diameter where a tree growing in uneven-sized stand reaches its maximum diameter growth rate is around 15 cm for pine, 25 cm for spruce and 20 cm for birch. Site fertility and temperature sum increase growth rate.



Fig. 1. Dependence of 5-year diameter increment on dbh and forest site type in pine, spruce and birch.



Fig. 2. Dependence of 5-year diameter increment of spruce on competition (*BAL*, stand basal area) and temperature sum on different sites.

3.2. Height model

The height model was a modification of the Hossfeld model (e.g., Björn and Kiviste, 1997):

$$h = \frac{a_1 + a_2 M T^+ + a_3 V T + a_4 C T + a_5 C l T}{1 + (b_1/d) + (b_2/d^2)}$$
(3)

Table 4

Parameters of the height models (Eq. (3)).

Variable	Pine	Spruce	Birch
Constant	25.014	33.726	29.375
MT ⁺	7.680	5.965	7.714
VT	6.376	2.178	3.059
CT	-1.787	-1.399	-2.870
CIT	-3.296	-	-
1/d	19.260	25.683	22.640
$1/d^2$	31.721	37.785	-8.000
No. of observations (trees)	8,622	12,144	1,200
R^2	0.779	0.856	0.802
Standard deviation of residuals	2.360	2.104	2.001



Fig. 3. Dependence of the height of spruce on dbh and growing site.

where *h* is tree height (m) and *d* is the diameter at breast height (cm). MT^+ is an indicator variable, which equals 1 if the site type is *Myrtillus* or better (otherwise $MT^+ = 0$). The model coefficients (Table 4) indicate that a tree of a certain diameter is shorter on poorer sites (Fig. 3).

3.3. Survival model

The survival model was as follows:

$$p_6 = \frac{1}{1 + \exp[-(a_1 + a_2\sqrt{d} + a_3\ln G + a_4BAL_{\text{Spruce}} + a_5BAL)]}$$
(4)

where p_6 is the probability of survival for the following 6-year period. The coefficients of the model (Table 5) show that large trees survive better than small ones (Fig. 4), and trees facing much competition have the smallest probability of surviving. The 6-year survival probability can be converted into 5-year probability as follows: $p_5 = p_5^{5/6}$.

The area under the ROC curve (receiver operating characteristic curve) was 0.89 for the spruce model and 0.93 for the model of other species (Fig. 5). Taking into account that a relative area equal to 1 indicates perfect fit and an area of 0.5 a useless model, these values are rather good. The percentage of correct predictions was the highest when 0.6 was used as the threshold probability (when trees with predicted probability greater than 0.6 were taken as survivals, see Fig. 5).

3.4. Ingrowth model

The ingrowth model gives the number of those trees that pass the 5 cm dbh limit during the following 5-year period. Similar to the survival models, one model was fitted for spruce and the other for pine and birch trees. The model form was:

$$\ln(\ln + 1) = a_1 + a_2\sqrt{G} + a_3\ln(G) + a_4\sqrt{N_{\text{Spruce}} + a_5\sqrt{N_{\text{Other}}}} + a_6MT^-$$
(5)

Table 5	
Parameters of the survival	models (Eq. (4)).

Variable	Spruce	Other
Constant	4.418	0.496
\sqrt{d}	1.423	1.649
În G	-1.046	-
BALSpruce	-0.0954	-
BAL	-	-0.106
Number of living trees in data	10545	3230
Number of dead trees in data	1127	289
Best threshold probability	0.5-0.6	0.6
Percentage of correct predictions	90.7	92.6



Fig. 4. Dependence of the probability of a tree to survive for 5 years on breast height diameter.



Fig. 5. The receiver operating characteristic curves of the survival models (top) and the percentage of correct predictions as a function of the predicted survival probability above which trees are taken as survivals (bottom). False alarm rate is the proportion of wrong survivals (dead trees predicted as survivals) and hit rate is the proportion of correct survivals (survivals predicted as survivals).

where *In* is the number of ingrowth (trees per hectare), N_{Other} is the number of non-spruce trees (dbh > 5 cm) per hectare and N_{Spruce} is number of spruce trees per hectare (dbh > 5 cm). *MT*⁻ is an indicator variable for sites which are *Myrtillus* type or poorer. *G* is the basal area of trees larger than 5 cm dbh (m² ha⁻¹). Table 6 and Fig. 6 show that an increase in stand basal area decreases ingrowth

Table 6

Parameters of the ingrowth models (Eq. (5)).

Variable	Spruce	Other
Constant	4.688	6.154
\sqrt{G}	-0.712	-
În G	_	-1.683
$\sqrt{N_{\text{Sruce}}}$	0.083	-
/N _{Other}	_	0.0642
MT -	-0.567	-
No. of observations (plots)	371	371
R ²	0.403	0.387
Standard deviation of residuals	1.700	1.559

The predicted variable is $\ln (\text{Ingrowth} + 1)$. The Baskerville correction factor has been added to the constant due to logarithmic transformation of the predicted variable.

whereas increasing number of trees increases it (see Buongiorno and Michie, 1980).

The model for the diameter of ingrowth trees was as follows:

$$\ln(D) = a_1 + a_2 \ln(G) + a_3 MT + a_4 VT^{-}$$
(6)

where *D* is the mean diameter of ingrowth at the end of the 5-year period. VT^- is an indicator variable which equals 1 if the site type is *Vaccinium* or poorer. The model (Table 7) predicts smaller diameters for stands with high basal area, i.e., increasing stand basal area decreases the diameter growth of ingrowth.

4. Simulation examples

The developed model set was used to simulate stand development for analyzing the effect of post-cutting stand density and the shape of post-cutting diameter distribution on stand dynamics and productivity. A one-hectare plot representing a pure spruce stand on *Oxalis-Myrtillus* site (*OMT*) was used in simula-



Fig. 6. Dependence of the number of 5-year ingrowth on stand basal area and number of trees per hectare (with dbh > 5 cm).

Table 7

Parameters of the models for the mean diameter of ingrowth (Eq. (6)).

Variable	Spruce	Other
Constant	2.004	1.958
ln G	-0.101	-0.0841
MT	-0.0176	-0.0425
VT -	-0.0646	-0.0556
No. of observations (plots)	170	141
R ²	0.586	0.469
Standard deviation of residuals	0.0473	0.0730

Predicted variable is natural logarithm of diameter.

tions. The plot had 1074 trees per hectare (dbh > 5 cm), stand volume of 162 m³ ha⁻¹ and basal area of 20 m² ha⁻¹. It was uneven-sized (Fig. 7). The temperature sum of the region was 1200 d.d., latitude 6800 km N, and elevation 50 m a.s.l. (Central Finland).

One 5-year time step was simulated as follows:

- Calculate the survival probability for each tree and take the tree as a survivor if its survival probability is greater than a uniform random number U[0,1].
- Calculate diameter increment for each tree and add it to the current diameter.
- Update tree heights using the height model.
- Predict the number, initial diameter and height of ingrowth trees.
- Add new trees to the plot corresponding to the predicted ingrowth.

In a cutting treatment the stand was thinned to a specified remaining basal area aiming at specified post-cutting *q*-ratios. It was not always possible to reach both the target basal area and the target values of *q*-ratios. This happened especially if the remaining basal area was high. In these cases, the target remaining basal area was given the first priority. The usual consequence of a too high basal area was that the *q* ratios were smaller than the target value among the smallest diameter classes, i.e., there were too few small trees and too many large ones in the post-cutting stand.

4.1. Effect of stand density

In the first set of simulations, the plot was thinned to the following remaining basal areas: 24, 20, 16, 12 and 8 m² ha⁻¹. The target *q* ratio of the post-cutting stand was 1.6 for all pairs of 4-cm-wide diameter classes. The simulation period was 100 years, and the cutting interval 10 years (the stand was thinned in years 5, 15,



Fig. 7. Initial diameter distribution of the stand used in simulation examples and the final distributions at the end of 100-year simulation with different remaining stand basal areas $(G, m^2 ha^{-1})$. The *q*-values in parentheses are the realized average *q*-values at the end of the 100-year simulation period, i.e., 5 years after the last cutting. The target *q*-ratio of the post-thinning stand was 1.6 for all diameter classes.



Fig. 8. Development of number of trees per hectare and quadratic mean diameter on *Oxalis-Myrtillus* site when the remaining basal area is 24, 16 or $8 \text{ m}^2 \text{ ha}^{-1}$ and cutting cycle is 10 years.

25, ..., 95). The mean annual harvest was calculated from the last 80 years assuming that the two first cutting cycles are required to transform the stand to the specified structure.

The simulation results show that all regimes maintained the stand as uneven-sized (Fig. 7). However, the highest post-thinning basal area, $24 \text{ m}^2 \text{ ha}^{-1}$, resulted in a slightly lower average q ratio (1.46) suggesting that this stand density is too high to enable a sufficient number of small trees. This is partly because of insufficient ingrowth and increased mortality rate among the smallest trees.

The stand dynamics was quite different for different postthinning stand densities (Fig. 8). The number of living trees in the stand trees varied much less with post-thinning basal area of $24 \text{ m}^2 \text{ ha}^{-1}$ as compared to 16 and 8 m² ha⁻¹. The mean tree size (quadratic mean diameter) was clearly larger with $24 \text{ m}^2 \text{ ha}^{-1}$ than with the other post-thinning basal areas. Many more trees were harvested with low remaining basal areas but the mean size



Fig. 9. Effect of remaining basal area on the productivity of an uneven-sized spruce stand on *Oxalis-Myrtillus* site with 10-year cutting cycle. The *q*-ratio of the post-thinning stand is 1.6 for all 4-cm diameter classes.



Fig. 10. Combinations of *q* ratios (q1/q2/q3) used in simulations: q1 dbh < 17 cm; q2 dbh 17-21 cm/21-25 cm; q3 dbh > 25 cm.

of harvested trees was smaller. The ingrowth was also much higher with low post-thinning basal areas.

The mean annual harvest was somewhat lower with postcutting basal areas of 20 and $24 \text{ m}^2 \text{ ha}^{-1}$ than with the other basal areas indicating that these densities are too much for the productivity of an uneven-sized stand growing on *OMT* in Central Finland (Fig. 9). This is because of lacking ingrowth, mortality among the smallest diameter classes, and small diameter increment due to heavy competition. The other stand densities had nearly the same mean annual harvest with the peak at $12 \text{ m}^2 \text{ ha}^{-1}$. The results suggest that, within a rather large range, the productivity of an uneven-sized spruce stand is not very sensitive to stand basal area. Decreasing remaining stand basal area increased the share of pulpwood, which decreases the monetary value of the harvest. With remaining stand basal areas of 8–20 m² ha⁻¹ the mean annual harvest of sawlog and pulpwood was 5.2–5.6 m³ ha⁻¹.

4.2. Effect of q ratio and cutting cycle

The same plot as in the previous example was used to study the effect of q ratio and the length of cutting cycle on the dynamics and productivity of an uneven-sized stand. The remaining basal area was $14 \text{ m}^2 \text{ ha}^{-1}$ with 10-year cutting cycle, $12 \text{ m}^2 \text{ ha}^{-1}$ with 20-year cycle, and $10 \text{ m}^2 \text{ ha}^{-1}$ with 30-year cycle. Four different sets of post-thinning q ratios were used with every cutting cycle (Fig. 10). A set of q ratios consisted of three q values, one for 4-cm diameter classes less than 17 cm, another for diameter classes 17-21 and 21-25 cm, and the third one for diameter classes larger than 25 cm. The mean annual harvest was calculated from 100-year simulation period but excluding the first cycles which were assumed to be required to convert the stand to the specified structure. Therefore, the yield estimates represent sustainable and steady-state situations.

The results clearly suggest that it is more profitable to harvest large diameter classes more heavily than small ones (Fig. 11). Of the compared sets of *q* ratios, 1.2/10.0/4.0 was the the best in terms of mean annual harvest. Both sawlog and pulpwood production increased when cuttings were directed more to large trees. With a short cutting cycle (10 years), the increase was higher in pulpwood but with a long cutting cycle (30 years) sawlog production increased more. From the mean annual harvests (Fig. 11) it can be calculated that the harvested volume per cutting was 55–68 m³ ha⁻¹ with 10-year cutting cycle, 105-129 m³ ha⁻¹ with 20-year cutting cycle, and 156-187 m³ ha⁻¹ with 30-year cutting cycle. The mean annual harvest was higher with a shorter cutting cycle but, on the other hand, the cutting operation would cost less per harvested cubic meter if the cutting cycle is longer, due to larger removal.



Fig. 11. Effect of *q* ratio on the productivity of an uneven-sized spruce stand on *Oxalis-Myrtillus* site with a cutting cycle of 10 (top), 20 (middle) and 30 (bottom) years. The three *q* ratios on the *x* axis (e.g., 1.6/1.6/1.6) stand for 4-cm diameter classes of the following dbh ranges: dbh < 17 cm (*q*1); dbh 17–21 cm/21–25 cm (*q*2); dbh > 25 cm (q3).

5. Discussion

The study presents the first complete set of models for simulating the dynamics of uneven-sized stands in Finland. The application area of the model set covers all main tree species and growing sites in the whole country. As demonstrated in the simulation examples, the models can be used to provide decision support in a variety of problems related to the management of uneven-sized stands. In addition to just simulating the outcome of alternative management regimes, the models can be used to optimize the management of uneven-sized stands. The objective variable in these optimizations could be timber production or economic profitability.

The models presented in this study predict maximum sustainable annual harvests of $6-7 \text{ m}^3$ /ha for good spruce sites (*OMT*) in Central Finland and $7-8 \text{ m}^3$ /ha in South Finland. For uneven-aged pine growing on medium site (*MT*) the models predict sustainable harvests of around 4 m^3 /ha in Central Finland and 4.5 m^3 /ha in South Finland. These yields are somewhat (around 0.5 m^3 /ha) less than in regularly thinned even-aged stands (e.g., Tapion taskukirja, 2002), most probably due to the rather low basal areas of uneven-aged stands. Low basal areas are necessary for ingrowth. However, the profitability of uneven-sized forestry would most probably be competitive with even-aged forestry and the low opportunity cost (low cost of capital) of the post-cutting stand.



Fig. 12. Comparison of predicted diameter increments of spruce in Cenral Finland obtained with the OLS model and the fixed part of a mixed model (fixed).

Representative Finnish NFI-data, long-term field experiments, and subjectively placed temporal plots were used for modeling the dynamics of uneven-sized forests. Mixing of different data sets brings some limitations to the modeling process. For instance, the possible temporal correlation of observations in one of the three data sets was ignored since there was no temporal correlation in the other data sets. However, temporal correlation may not be a significant problem with 5-year growth intervals (Gertner, 1985; Quicke et al., 1994). The fact that trees of the same plot are correlated observations was also ignored. This does not cause any bias in the regression coefficients but the statistical significance of the coefficients is overestimated (e.g., Quicke et al., 1994). Despite these problems, it was realized that all data sets were required to develop models for all main tree species and for the whole country.

The correlation between observations of the same plot could have been taken into account by fitting a random parameter model (also called mixed model) with random factors for both betweenplot and within-plot variation. In fact, diameter increment models of this model type were fitted in the course of the study. The mixed models were rather similar as the OLS models (Fig. 12) but the statistical significance of predictors which are constant within a plot (stand basal area, site variables) was lower because the plot factors explained a part of the effect of these variables. The mixed models had a smaller RMSE than the OLS models (e.g., 0.505 for spruce compared to the RMSE of 0.604 of the OLS model). However, the fixed part of the mixed model had a larger RMSE (0.614 for spruce). Therefore, since the plot factor is seldom estimated when the models are used (only the fixed model part is used, or plot factor is taken as zero), it was concluded that the OLS models are better for forestry practice than the mixed models.

The data set used to model diameter increment is very large. The relationships between diameter increment and predictor variables were rather similar in all three data sets. Therefore, it may be concluded that the diameter increment models reliably show the level of diameter increment in uneven-sized stands. Mortality is a less significant factor in regularly thinned stands. Therefore, the survival models are a less critical component of the model set. The height models are based on a reasonably large data set. In addition, the static height models do not affect the simulated stand dynamics since height never appears as a predictor in the increment, ingrowth and survival models. Height models are only required to predict tree volume, and possible errors in height models bring bias in volume estimates but they do not invalidate conclusions about, for instance, the sustainability of different management schedules.

When the models are used in simulation, individual trees or diameter classes of trees may represent the stand. In the latter alternative, each diameter class is typically represented by one tree, characterized by diameter, height, and frequency (number of trees per hectare). Mortality is most conveniently simulated by multiplying the frequencies of trees by their survival probability (Vanclay, 1994). When individual trees are used, a decision needs to be taken whether a tree survives during the following few years (time step of the model) or not. Trees having a predicted survival probability greater than a threshold probability are survivals. The best threshold value turned out to be 0.6 for all species. Another possibility to use the mortality models in individual-tree simulation is stochastic: the predicted survival probability of a tree is compared to a uniformly distributed random number and the tree is taken as a survivor if its survival probability is greater than the random number. This option was used in the simulation examples of this study.

The ingrowth models are by far the weakest part of the developed model set. The data used to model ingrowth consisted of 371 observations only, which is a small number compared to the other models. There is a possibility that a part of the ingrowth data was not representative for uneven-sized stands. For example, the treatment history of the Karelia plots was unknown, and it is possible that some clearing of small trees had taken place in some plots, reducing the ingrowth. However, the analysis of the data did not indicate that the level of ingrowth is less in the Karelia data than in the Honka-Vessari data. Ingrowth is of crucial importance for the sustainability and long-term productivity of uneven-sized stands. Without sufficient recruitment the stands will turn even-sized and their volume growth decreases as the trees get older. Therefore, acquiring more information on the ingrowth of uneven-sized stands is an obvious way to improve the model set.

According to the models, thinning large trees more heavily than small ones would increase ingrowth, which correlates positively with the number of trees and negatively with stand basal area. Infrequent heavy thinnings may be better for ingrowth than frequent light thinnings. They also improve the net return of harvesting operations. In the simulation examples, the removal was about $60 \text{ m}^3 \text{ ha}^{-1}$ with 10-year cutting cycle, $120 \text{ m}^3 \text{ ha}^{-1}$ with 20-year cutting cycle, and $170 \text{ m}^3 \text{ ha}^{-1}$ with 30-year cutting cycle. In southern Finland, cuttings with removal exceeding $100 \text{ m}^3 \text{ ha}^{-1}$ are regarded profitable (Lähde et al., 1999).

One way to promote ingrowth is to make the stand spatially heterogeneous, i.e., a mosaic of dense and sparse places. Sparse places will get ingrowth while dense places can be heavily thinned and converted into new sparse places. Another option is to make the management temporally heterogeneous, i.e., conduct a set of very heavy cuttings to promote regeneration and ingrowth, after which there is a period of light cuttings to increase yield, which is again followed by a period of heavy cuttings.

The long-term field experiments and the NFI3 plots used as modeling data in this study, have revealed an abundance of seedlings, saplings and other understory trees in uneven-sized stands (Lähde et al., 1999; Eerikäinen et al., 2007). Other field experiments have also found rich conifer regeneration (Lähde, 1992a; Lundqvist, 1993; Lundqvist and Fridman, 1996). However, birch regeneration in uneven-sized Norway spruce-dominated forests suffers as growing stock volume increases (Lähde, 1992a). This can be overcome by lowering basal area considerably. Regeneration of light demanding trees can be promoted also by scarifying the soil and creating wide enough gaps in the canopy. One option, but costly, is enrichment planting (Hagner, 1992).

According to the models developed in this study, uneven-sized stands provide a fair increment and render a good saw-timber yield. The rotated-sigmoid form of the diameter distribution (Goff and West, 1975; Schütz, 1989) maximizes the harvest of log-sized trees and guarantees a high transition of new trees into valuable size classes during the next cutting cycle. The simulation examples indicate that the total and sawlog yields are of the same magnitude with many stand densities and shapes of diameter distribution. The models therefore support the view that certain stand structures and cutting regimes need not be closely followed (O'Hara, 1996). Uneven-sized forests do not even need to follow the reversed J-curve (O'Hara, 1996, 1998) as long as the stand density is kept roughly at the right level. It seems to be enough to maintain the target stand density and shape of diameter distribution only approximately. The key point in the management of uneven-sized forests is to guarantee sufficient regeneration and ingrowth.

References

- Björn, E., Kiviste, A., 1997. Construction of site index equations for *Pinus sylvestris L.* using permanent sample plots data in Sweden. Forest Ecology and Management 98, 125–134.
- Buongiorno, J., Michie, B.R., 1980. A matrix model of uneven-aged forest management. Forest Science 26 (4), 609–625.
- Cajander, A.K., 1949. Forest types and their significance. Acta Forestalia Fennica 56, 1–71.
- Cancino, J., Gadow, K.V., 2002. Stem number guide curves for uneven-aged forests development and limitations. In: Gadow, K.V., Nagel, J., Saborowski, J. (Eds.), Continuous Cover Forestry—Assessment, Analysis, Scenarios. Managing Forest Ecosystems, vol. 4. pp. 163–174.
- Daniel, V., Helms, J.A., Baker, F.S., 1979. Principles of Silviculture, 2nd edition. McGraw-Hill, New York, p. 500.
- Eerikäinen, K., Miina, J., Valkonen, S., 2007. Models for the regeneration establishment and the development of established seedlings in uneven-aged Norway spruce dominated stands of southern Finland. Forest Ecology and Management 242, 444–461.
- Gertner, G.Z., 1985. Efficient nonlinear growth model estimation: its relationship to measurement interval. Forest Science 31 (4), 821–826.
- Goff, F.G., West, D., 1975. Canopy–understory interaction effects on forest population structure. Forest Science 21, 98–108.
- Groot, A., Gauthier, S., Bergeron, Y., 2004. Stand dynamics modeling approaches for multicohort management of eastern Canadian boreal forests. Silva Fennica 38 (4), 437–448.
- Hagner, M., 1992. Biologiskt och ekonomiskt resultat i fältförsök med plockhuggning kombinerad med plantering. In: Abstract: Biological and Economical Results from Experiments with Selective Felling Combined with Enrichment Planting. Working Paper 63, Department of Silviculture, The Swedish University of Acricultural Sciences, pp. 52.
- Huse, S., 1965. Strukturformer hos urskogsbestand in Øvre Pasvik. Referat: Strukturformer von Urwaldbeständen in Övre Pasvik. Meldingar fra Norges Landbrukshøgskole 44 (31), 1–81.

- Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H., Haapala, P., 2002. Models for predicting stand development in MELA system. Finnish Forest Research Institute, Research Papers 835, pp. 116.
- Hytteborn, H., Packham, J.R., Verwjist, T., 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibäcken, northern Sweden. Vegetatio 72, 3–19.
- Ilvessalo, Y., 1951. III valtakunnan metsien arviointi. Suunnitelma ja maastotyön ohjeet. Summary: Third national forest survey in Finland. Plan and instructions for field work. Communicationes Instituti Forestalis Fenniae 39 (3), 1–67.
- Lähde, E., 1992a. Natural regeneration of all-sized spruce-dominated stands treated by single tree selection. In: Hagner, M. (Ed.), Silvicultural Alternatives. Proceedings from an Internordic Workshop, June 22–25, 1992. Department of Silviculture, Swedish University of Agricultural Sciences (Reports, 35, pp. 117–123).
- Lähde, E., 1992b. Nature oriented silviculture in an ecocommune. In: Heikurainen, K. (Ed.), Suomussalmi Ecomunicipality. Suomussalmi Municipality, pp. 44–50.
- Lähde, E., Laiho, O., Norokorpi, Y., Saksa, T., 1991. The structure of advanced virgin forests in Finland. Scandinavian Journal of Forest Research 6, 527–537.
- Lähde, E., Laiho, O., Norokorpi, Y., 1999. Diversity-oriented silviculture in the Boreal Zone of Europe. Forest Ecology and Management 118, 223–243.
- Lundqvist, L., 1993. Changes in the stand structure on permanent *Picea abies* plots managed with single-tree selection. Scandinavian Journal of Forest Research 8, 510–517.
- Lundqvist, L., Fridman, E., 1996. Influence of local stand basal area on density and growth of regeneration in uneven-aged *Picea abies* stands. Scandinavian Journal of Forest Research 11, 364–369.
- Miina, J., Pukkala, T., 2000. Using numerical optimization for specifying individualtree competition models. Forest Science 46 (2), 277–283.
- Nilsson, N.-E., Östlin, E. 1961. Rikskogstaxeringen 1938–1952. Forest inventory 1938–1952. Avdelningen för skogstaxering. Rapporter 2, pp. 162.
- O'Hara, K.L., 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. Forest Science 42 (4), 1–34.
- O'Hara, K.L., 1998. Silviculture for structural diversity: a new look at multiaged systems. Journal of Forestry 96 (7), 4–10.
- Palahí, M., Pukkala, T., Kasimiadis, D., Konstantinos, P., Papageorgiou, A.C., 2008. Modelling site quality and individual-tree growth in pure and mixed *Pinus brutia* stands in north-east Greece. Annals of Forest Science 65 (5) 501p1– 501p14.
- Peng, C., 2000. Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management 132, 259–279.
- Porté, A., Bartelink, H.H., 2002. Modelling mixed forest growth: a review of models for forest management. Ecological Modelling 150, 141–188.
- Pukkala, T., Kolström, T., 1988. Simulating the development of Norway spruce stands using transition matrix. Forest Ecology and Management 25, 255–267.
- Pukkala, T., Miina, J., 1998. Tree-selection algorithms for optimizing thinning using a distance-dependent growth model. Canadian Journal of Forest Research 28, 693–702.
- Pukkala, T., Miina, J., Kurttila, M., Kolström, T., 1998. A spatial yield model for optimizing the thinning regime of mixed stands of *Pinus sylvestris* and *Picea abies*. Scandinavian Journal of Forest Research 13, 31–42.
- Quicke, H.E., Meldahl, R.S., Kush, J.S., 1994. Basal area growth of individual trees: a model derived from a regional longleaf pine growth study. Forest Science 40 (3), 528–542.
- Schütz, J.-Ph., 1989. Der Plenterbetrieb. Fachbereich Waldbau ETH, Zürich, p. 54.
- Snowdon, P., 1991. A ratio estimator for bias correction in logarithmic regressions. Canadian Journal of Forest Research 21, 720–724.
- Tapion taskukirja, 2002. Handbook of Forestry Development Centre Tapio, in Finnish. Publ. by Metsälehti Kustannus. Gummerus Kirjapaino Oy, Jyväskylä, 555 p.
- Tarasink, S., Zwiernirski, M., 1990. Social-structure dynamics in uneven-aged Scots pine (*Pinus sylvestris*) regeneration under canopy at the Kaliszki Reserve, Kampinoski National Park (Poland). Forest Ecology and Management 35, 277–289.
- Trasobares, A., Pukkala, T., 2004. Using past growth to improve individual-tree diameter growth models for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain. Annals of Forest Science 61, 400– 417.
- Trasobares, A., Pukkala, T., Miina, J., 2004. Growth and yield model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain. Annals of Forest Science 6, 9–24.
- Vanclay, J., 1994. Modelling Forest Growth and Yield. Applications to Mixed Tropical Forests. CAB International, Wallingford, UK, ISBN: 0 85198 913 6, 312 pp.
- Westphal, C., Tremer, N., von Oheimb, G., Hansen, J., von Gadow, K., Härdtle, W., 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? Forest Ecology and Management 223, 75–83.
- Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. Forest Science 36, 1077–1104.
- Zackrisson, O., Nilsson, M.-C., Steijlen, I., Hörnberg, G., 1995. Regeneration pulses and climate-vegetation interactions in non-pyrogenic boreal Scots pine stands. Journal of Ecology 83, 1–15.