Forest Ecosystems
a SpringerOpen Journal

RESEARCH   **Open Access**

Ingrowth, survival and height growth of small trees in uneven-aged *Picea abies* stands in southern Finland

Kalle Eerikäinen[1*], Sauli Valkonen[2] and Timo Saksa[3]

Abstract

The purpose of the study was to analyse height growth, mortality, and ingrowth of individual small-sized trees in uneven-aged spruce-dominated stands. It was based on experimental data from 16 stands for a 15-year observation period including four measurements with a 5-year interval. In the data of this study, the heights of small-sized trees varied from 0.1 to about 9 m. Results showed that the growth of small trees was rather slow, particularly in the smallest size classes. With average growth rates it would take about 60 years for a freshly emerged spruce germinant to achieve 1.3 m in height. The stand density, site quality and selection cuttings affected the growth of small-sized spruces. Average five-year mortality rates for spruce, birch and pine were 17.0%, 40.9% and 33.9%, respectively. Annual ingrowth rates with the threshold height of 1.3 m for the three species were on average 30.4, 2.8 and less than 0.1 trees per hectare, respectively. Even if, a selection cutting of modest intensity (25% of basal area removed on average) seemed to have accelerated the growth of small spruces, it is recommended that more intensive harvestings be applied to enhance the survival and growth of small spruces. It is also concluded that shade intolerant species like birch and pine do not seem to be capable of developing into viable undergrowth in spruce selection stands with their current levels of stand density.

Keywords: Growth; Regeneration; Selection cutting; Silviculture; Uneven-aged forest

Background

One of the key dynamic components of sustainability in uneven-aged forest management is the survival and development of the small trees, which are often labelled regeneration, seedlings and sapling in practical terms with variable definitions. Their recruitment, survival and ability to withstand long suppression periods and recover after release are crucial to attaining and maintaining ecologically and economically sustainable stand structures.

The emphasis of studies on uneven-aged management has been on estimating growth and yield of larger trees and optimizing their cutting treatments. The data sets and results of the studies on regeneration and tree development have been rather limited in size, scope, and coverage of the potential sources of variation. Consequently, our knowledge on the related processes is still

rather limited. It has been a weak point in studies assessing the feasibility of uneven-aged management in the Nordic countries (Kolström, 1993; Lundqvist, 1993, 1995; Wikström, 2000, 2008; Andreassen and Öyen, 2002; Miina et al., 2006; Lundqvist et al., 2007; Gobakken et al., 2008; Lexerød, 2008; Pukkala et al., 2009, 2010; Tahvonen, 2009; Tahvonen et al., 2010). Due to the fact that the models used have been rather rudimentary and of limited reliability in simulation studies, it has been difficult to assess the reliability of the optimization results particularly on what comes to the long-term sustainability and productivity of the simulated practices.

The principal factors driving emergence, mortality and growth of new trees in Norway spruce stands with relatively high canopy closure include: seed crop, seedbed properties, climatic factors and competition from ground vegetation and larger trees (Clarke, 1992; Pukkala and Kolström, 1992; Örlander and Karlsson, 2000; Hanssen, 2002, 2003; Chantal et al., 2003; Hanssen et al., 2003; Valkonen and Maguire, 2005). Regeneration surveys on

* Correspondence: kalle.eerikainen@metla.fi
[1]Finnish Forest Research Institute, Joensuu Unit, P.O. Box 68, FI-80101 Joensuu, Finland
Full list of author information is available at the end of the article

experimental plots and their analyses have provided some basic knowledge on the number and distribution of germinants, seedlings, and saplings in uneven-aged spruce stands in the Nordic countries (Lundqvist, 1989, 1991; Lundqvist and Fridman, 1996; Nilson and Lundqvist, 2001; Saksa, 2004; Eerikäinen et al., 2007; Lundqvist et al., 2007; Saksa and Valkonen, 2011). Compared to their emergence, less attention has been paid to the details of survival and development of established small trees in uneven-aged stands in the area. So far, datasets have been limited in terms of the number of plots and the length of observation periods.

After the emergence stage, competition by the existing larger trees is assumed to become a more and more decisive factor that affects the growth of small trees and their ingrowth into the main canopy (Lundqvist and Fridman, 1996; Nilson, 2001; Nilson and Lundqvist, 2001; Saksa, 2004; Eerikäinen et al., 2007; Lundqvist et al., 2007). However, Lundqvist (1989, 1991) and Lundqvist and Fridman (1996) found that the influence of local and stand-level density had no or only a very weak effect on the growth of small trees in uneven-aged spruce stands in northern and central Sweden, whereas Chrimes and Nilson (2005) reported negative influences which occurred in the very North. In addition, small trees are often damaged and destroyed in harvesting (Fjeld, 1998; Granhus, 2001; Granhus and Fjeld, 2001; Surakka and Sirén, 2007; Surakka et al., 2011).

In many simulation models, tree emergence, survival and growth have been aggregated into lump estimation of ingrowth at a certain diameter threshold. The threshold diameter has varied from 0 to 8.5 cm in studies conducted in central and northern Sweden (Lundqvist, 1989, 1993; Lundqvist et al., 2007) and to that of 5 cm used in Norway (Lexerød, 2005). For practical purposes, it could be sufficient to predict ingrowth, but the current procedures tend to be too simplistic for realistic simulation, particularly while ignoring the spatial and temporal variation of survival, growth, and distribution of regeneration which can be very large (Saksa, 2004; Saksa and Valkonen, 2011).

The Finnish Forest Research Institute has conducted detailed investigations on tree emergence, growth and mortality processes in its ongoing research on single-tree selection using a set of experimental plots entitled "ERIKA". Saksa (2004), Valkonen and Maguire (2005) and Saksa and Valkonen (2011) utilized data collected from the ERIKA plots for examining the initial stages of the process (tree emergence, survival, and growth up to 1.3 m height) with respect to measured stand-level attributes, whereas Eerikäinen et al. (2007) modelled regeneration dynamics and tree development. The data contained just one 5-year observation period, and the models were therefore deemed preliminary. So far, a less

detailed description for the response to harvesting has been obtained, for instance.

The main objective of this study was to establish an empirical basis for modelling the dynamics of the small-tree cohorts in uneven-aged Norway spruce stands in southern Finland. We explored and analysed height growth, mortality and ingrowth by expecting tree size and species, site type, and stand density (basal area) to be significant factors. These characteristics form a basis for the operational modelling, in which different tree- and stand-level models are to be synchronized in to a compatible simulation system needed for predicting the development of uneven-aged spruce stands. Another objective was to present and interpret our observations for the benefit of respective research under quite similar conditions in the Nordic area, particularly for cross-checking purposes.

Methods

The study material was acquired from a set of 16 experimental plots in southern Finland (61° 00′ N – 62° 00′, 25° 00′ – 27° 30′ E) at four locations, namely Vesijako (VES), Lapinjärvi (LAP), Evo (EVO), and Puolivälimäki in Vesijako (VEP). The plots had been explicitly established for studies on tree and stand development in managed, uneven-aged Norway spruce forests conducted under the 'ERIKA' research project at the Finnish Forest Research Institute (Metla). The plots had been established in 1991–1992. The study sites were subjectively selected among about 40 candidate stands available for the project on the properties of Metla, Metsähallitus (administrator of state-owned forests in Finland), Evo School Forest, and a few other forest owners. Stands that displayed a great degree of resemblance with a classic single tree selection structure in terms of diameter distribution and homogenous spatial distribution were *a priori* assessed to have a potential to develop towards a sustainable selection structure. The stands represented various stages of transition to some future, yet undefined sustainable single tree selection structures. Their diameter distributions ranged widely, thus representing varying forest structures. Originally 21 plots were established. One stand (LAP8) was completely destroyed by a tornado in 1998, and therefore its data were excluded from this analysis. In addition, data from four plots in Suonenjoki (SUO1, SUO2, SUO3 and SUO6) were discarded in this study due to their divergent measurement protocol: recordings for trees shorter than 1.3 metres were only available from the 64 circular regeneration plots within each of the four ERIKA plots.

The remaining 16 stands had been treated with selection cuttings of unknown intensity and interval during 1950–1980. In 1984–1988, they were all treated with single tree selection at a variable intensity. In 1996, a

selection cutting was carried out to enhance uneven-aged structures in 11 stands and to reset their basal areas to the original values of 1984–1988. The emphasis of removal was in the larger diameter classes ($d > 30$ cm). However, some larger trees had to be retained in many stands in order to achieve the target basal area. On the other hand, a number of mid-sized trees (20 cm $< d <$ 30 cm) were removed where there was an obvious surplus. The average basal area removal was 5.9 m^2 ha^{-1} (24.6%, see Table 1). Five stands were not harvested due to their operationally unjustifiable harvestable volumes. In three of these stands (VES13, VES14, VES16), only three years had passed since the previous cutting treatment, and in two of the stands (LAP1, EVO3) the operationally justifiable harvestable volume of 40 m^3ha^{-1} had not been attained due to slow growth during the first 8 years after the initial selection cutting.

The forest stands represented the most common spruce sites on mineral soil, i.e. mesic *Oxalis-Myrtillus* type (OMT) and submesic *Myrtillus* type (MT) (Cajander, 1926; see also Table 1). At the beginning and at the end of the monitoring period, on average, 71% and 77% of the total stand volume was comprised by spruce, respectively. The remaining portions of the stand volumes comprised of Scots pine (*Pinus sylvestris* L.) and various broadleaf species, mainly silver birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.) and aspen (*Populus tremula* L.).

In each stand, all measurements took place on a 40 m × 40 m plot. All trees taller than or equal to 0.1 m were described according to species and coordinates, and measured for diameter at breast height and height in 1991, 1996, 2001 and 2006. This study was based on a subset of data containing the observations of trees that were from 0.1 to 4.0 m high at the time of plot establishment and were measured with slightly different protocols compared to trees shorter than 0.1 m and taller than 4 m. The trees were measured with identical protocols at 5-year intervals. The data from 16 stands contained 14,685 individual trees with 1–3 observation periods of 5 years each. Only spruces (14,088), birches (484), pines (107), i.e. the species of commercial value, were studied. Measurements obtained for other tree species and collected from altogether 6 trees were discarded from the analysis due to the insufficient number of species-wise observations.

In data preparation, each tree was individually traced throughout its existence during the 15-year observation period. Its presence or absence (living, dead, or missing) and height were recorded at each of the four measurements. Height increment was obtained by calculating the difference between the individual tree heights measured at the end and at the beginning of each 5-year period. Negative values where accepted when they were proved to be genuine, since breakages or abscissions and regrowths of the leader shoots of birches, especially, were rather common. A survival was recorded if a tree

Table 1 Stand characteristics by the ERIKA plots at the beginning in 1991 and at the end in 2006 of the 15 years monitoring period

Area	Stand	Forest type	N, ha⁻¹		G, m²ha⁻¹		G_rem, %	V, m³ha⁻¹		Admixture, %	
			Beginning	End	Beginning	End		Beginning	End	Beginning	End
VES	1	MT	2194	2367	22.3	25.8	24.9	181.0	230.1	23.7	15.6
	2	MT	2675	1878	19.9	23.8	31.4	163.3	210.5	32.1	15.9
	5	MT	1827	1553	16.7	22.0	26.8	163.8	210.6	0.0	0.0
	7	MT	1459	1451	16.9	20.5	22.8	148.0	194.5	25.4	15.7
	13	MT	1211	1847	12.4	20.5	0.0	97.9	199.1	19.3	15.5
	14	OMT	723	1458	15.7	26.5	0.0	167.5	307.0	0.0	0.1
	16	MT	1888	1869	15.6	23.9	0.0	135.7	229.7	38.4	27.4
LAP	1	OMT	4428	2406	14.2	26.3	0.0	117.8	230.9	49.8	47.6
	5	OMT	1681	1808	34.9	32.8	30.4	371.3	361.5	71.5	77.6
	7	OMT	2786	3900	19.2	26.0	14.6	188.5	246.8	62.2	52.0
	13	MT	1528	2311	18.7	21.0	26.3	188.2	203.0	47.1	37.2
EVO	2	MT	900	956	17.4	18.7	21.4	171.7	186.5	29.4	26.3
	3	MT	731	1109	9.9	13.9	0.0	91.0	131.3	0.1	0.1
	4	MT	1881	1538	22.4	25.1	21.1	208.1	249.5	45.2	26.1
VEP	2	MT	606	631	18.3	21.1	23.9	179.2	218.7	0.1	0.0
	4	MT	1681	1713	19.8	22.6	27.2	187.1	219.1	13.4	3.7

OMT = *Oxalis-Myrtillus* Type and MT = *Myrtillus* Type according to Cajander (1926), N = number of stems for trees with height equal to or greater than 1.3 m, G = stand basal area, G_rem = basal area removal in 1996, V = stem volume, Admixture = proportion of stem volume obtained for other species than spruce.

was present and alive both at the beginning and at the end of the 5-year period. Since the second measurement in 1996 was carried out only prior to harvesting but not repeated after harvesting, part of the mortality during 1996–2001 is due to losses and damages caused by logging.

Relationships between tree height increment and survival during the 5-year intervals and between the measurements were analysed based on tabulation and illustration frameworks. In addition, correlation coefficients between tree attributes and potential explanatory variables such as site quality and basal area were calculated and inspected. A mixed-effects modelling-based regression analysis was also applied to elucidate the relationship between height growth and size of trees and to assess the magnitude of differences in mean growth estimates obtained by forest stands and growth periods. A nonlinear mixed-effects (NLME) modelling procedure was applied, especially because of its efficiency to account for random fluctuations arising from data: both spatially hierarchical (experimental plots or forest stands and trees) and temporally cross-sectional (growth periods) correlation structures were apparent in ERIKA data and, therefore, the basic assumption about uncorrelated error terms was unlikely to hold (see Pinheiro and Bates 2002). Parameters of the NLME model were estimated using the 'nlmer()' function in the lme4 package under the statistical software R (R Core Team 2012).
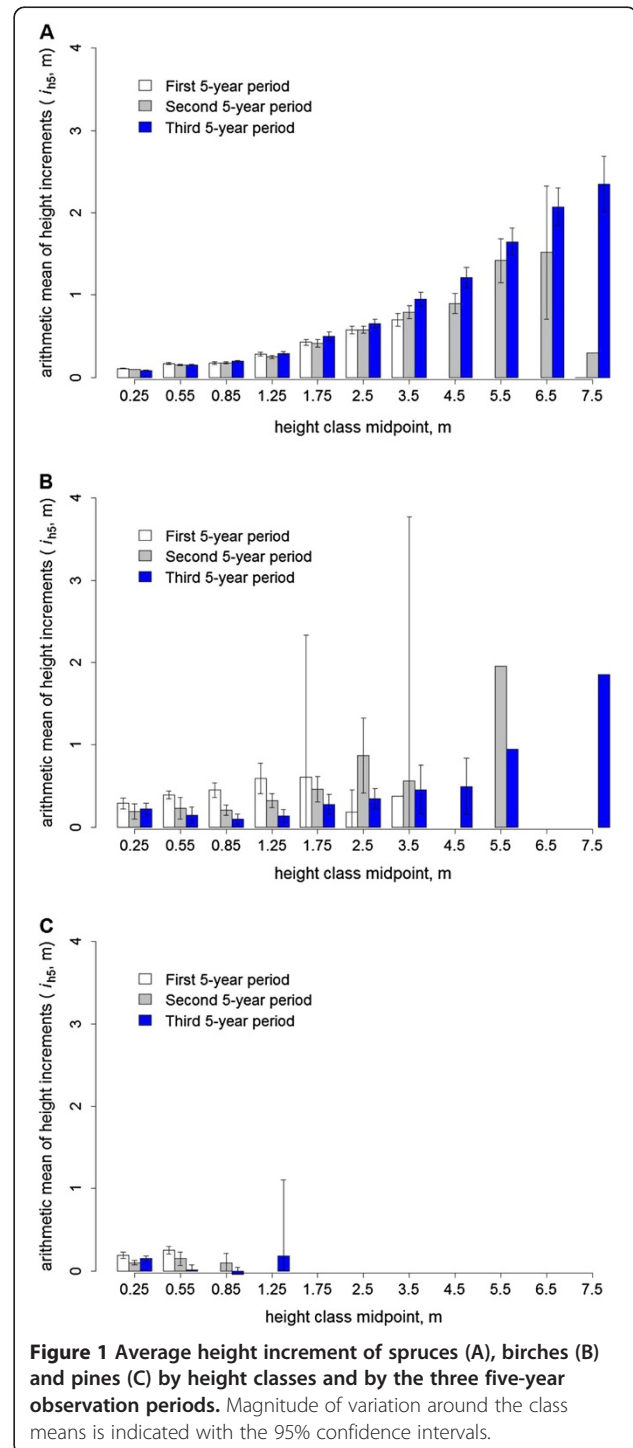
The t-test was used to assess the significance of fixed model parameters which were treated as significant at the levels of the p-value less than 0.05, whereas the significance test for the Maximum Likelihood (ML) estimated parameters obtained for random effects was based on the Likelihood Ratio Test (LRT) (see Goldstein 1995; Pinheiro and Bates 2002). The validation of candidate models, i.e. models with different combinations of independent variables used in their fixed model parts, was based on the ML estimated parameters by employing as criteria the Akaike Information Criterion, i.e. AIC values (Pinheiro and Bates 2002). After completing the comparisons made between different parametrisations the candidate models with ML estimated parameters, the REML estimates were obtained for the final parameterisation of the nonlinear mixed-effects model (Pinheiro and Bates 2002). In order to eliminate the possible sources of prediction bias, both the standardised and pure residuals were inspected using scatterplots that were obtained for the candidate models as functions of the independent variables and with and without the estimated random coefficients.

Results

Height increment

The 5-year height increment (i_{h5}) was very closely correlated with tree height (h) for spruce: greater height was generally associated with faster growth (Figure 1A).

Variation was very large though, which showed up in the correlation coefficient ($r = 0.672$, $p < 0.0001$) for h and i_{h5} and in the confidence intervals of aggregated height increments in the classes of tallest trees (Figure 1A). As seen in Figure 1B for birch, the increasing pattern in height increment was not as unambiguous as with spruce ($r = 0.171$, $p < 0.0001$; see also Figure 1A). Small

Figure 1 Average height increment of spruces (A), birches (B) and pines (C) by height classes and by the three five-year observation periods. Magnitude of variation around the class means is indicated with the 95% confidence intervals.

birches ($h < 0.4$ m) grew a bit faster than spruces having the same height. However, growth of taller spruces was faster when compared to birches of the same size class which was especially clear in the case of the third growth period. In addition, birch growth varied more than that of spruce. One essential factor was that a major proportion of birches showed negative growth, i.e. their tops had been broken or "wilted" between the measurements. Observations with negative increments were retained in the data because it seemed to be an essential feature in describing the process of tree height development. There were very few birches in the upper height classes in the ERIKA plots. For instance, the number of height growth observations for birches equal to or taller than 4.0 m by the 1st, 2nd and 3rd growth period were 0, 1 and 7, respectively. The correlation between height and height growth was weakly negative for pine ($r = -0.174$, $p = 0.017$; Figure 1C). The total absence of pine regeneration taller than 1.5 m throughout the three consecutive monitoring periods was very salient in the data.

Tree height growth was faster on the more fertile *Oxalis-Myrtillus* forest type (OMT) compared to that of the *Myrtillus* forest type (MT). Based on all increment observations in the data, the between-forest type mean ratios (OMT/MT) obtained for spruce, birch and pine were 1.67, 1.76 and 1.34, respectively. The species-specific ratios were rather consistent through the ranges of tree heights. Differences in height increments between the two site types and by the three species were also assessed using the Welch's t-test. Significant differences were obtained for spruce ($t = 22.725$, p-value < 0.0001) and birch ($t = 6.949$, p-value < 0.0001) that, however, did not hold for pine ($t = 0.852$, p-value $= 0.4201$).

A NLME model was constructed for assessing the relationship between the 5-year height increment and size of spruce and for verifying the significance of stand specific factors affecting the growth of trees. The small number of observations, combined with a high degree of random variation in the height growth, made the modelling pointless for birch and pine. The resulting predictor for height increment of the spruce tree j in forest stand (experimental plot) i and during the growth period t ($i_{\mathrm{h}5tij}$, m), and having a random intercept and slope term associated with random forest stand (u) effects was as follows:

$$
\begin{aligned}
i_{\mathrm{h}5tij} = \exp\big(& (\beta_0 + u_{0,i}) + (\beta_1 + u_{1,i}) \times \ln(h_{tij}) + \beta_2 \times \frac{1}{G_{ti}} \\
& + \beta_3 \times z_{\mathrm{OMT}i} + \beta_4 \times TI_i \times z_{\mathrm{PAT}1ti} + \beta_5 \times TI_i \times z_{\mathrm{PAT}2ti} \big) \\
& + e_{tij},
\end{aligned}
$$

for which　　　　　　　　　　　　　　　　　　　　　(1)

$$
\binom{u_{0,i}}{u_{1,i}} \sim N(\mathbf{0}, \mathbf{\Omega}_u) : \mathbf{\Omega}_u = \begin{pmatrix} \sigma^2_{u_0} & \sigma_{u_0 u_1} \\ \sigma_{u_1 u_0} & \sigma^2_{u_1} \end{pmatrix}
$$

$$
e_{tij} \sim N(\mathbf{0}, \sigma^2_e)
$$

where h_{tij} is tree height, m; G_{ti} is basal area, m^{2}ha^{-1}; $z_{\mathrm{OMT}i}$ is a forest stand-specific dummy variable for *Oxalis-Myrtillus* forest type (OMT), being 1 in the case of the respective forest type and 0 otherwise; TI_i is a forest stand-specific thinning intensity obtained as a ratio between the basal area removed in the thinning and the basal area before the thinning; $z_{\mathrm{PAT}1ti}$ and $z_{\mathrm{PAT}2ti}$ are dummy variables for the first and second 5-year period of growth after thinning, respectively; $\beta_0, ..., \beta_5$ are parameters for fixed effects; $u_{0,i}$ and $u_{1,i}$ are random parameters for forest stand effects; and e_{tij} is parameter for random errors of the model.

Stand basal area had a significant influence on tree height increment as indicated in Equation 1 (Table 2). Positive sign of the coefficient estimated for the dummy variable for the OMT forest type verified the trivial finding from the correlation analysis that the height growth on mesic forest sites was higher when compared to that on sub-mesic, i.e. MT, forest sites. The selective thinning had a twofold impact on the development of the modelled growth characteristic: during the first 5-year period it decreased and during the second period it increased the height increment. In addition, the thinning effect was dependent on the degree of thinning intensity. It is also worth considering here that the random tree effects were nonsignificant. Besides, the random parameters for cross-sectional time effects became nonsignificant when the thinning effects were specified in the fixed part of the model.

Equation (1) was applied to demonstrate the average, stand-specific height development patterns of spruce by utilising the estimates obtained for random stand-effects. A fixed time step of five years was used in simulation

Table 2 Estimates for the fixed parameters and random components of Equation 1

Fixed effects				
Parameter	**Estimate**	**Standard error**	***t*-value**	***p*-value**
β_0	−2.53262	0.04859	−52.13	< 0.0001
β_1	0.93862	0.01089	86.16	< 0.0001
β_2	16.39989	0.71418	22.96	< 0.0001
β_3	0.41721	0.03633	11.48	< 0.0001
β_4	−0.33940	0.07008	−4.84	< 0.0001
β_5	1.36607	0.06074	22.49	< 0.0001
Random forest stand effects				
	u_0	u_1		
u_0	4.1320×10^{-3}	−0.487		
u_1	-9.9498×10^{-4}	1.0102×10^{-3}		
Random errors				
	e			
e	5.0258×10^{-2}			

Estimates for random forest stand effects comprise variances (diagonal), covariances (lower triangle) and correlations (upper triangle), whereas random errors are specified by a variance estimate.

and measured, stand-specific values were used for basal area and thinning removal. In addition, an increment prediction was recursively added to tree height at each time step when predicting the height developments in average conditions of the 16 experimental stands, respectively.

Major between-stand growth variations were detected and included in the model. In the stand with the fastest growth observed (VES14), an initially 0.1 m tall spruce tree having an average, stand-specific growth rate would reach breast height ($h = 1.3$ m) at about 35 years (Figure 2). In the two stands with medium-growth rate (LAP1 and EVO2), 1.3 m would be reached after 55 years. It is expected, however, that for an average tree in the stand with the lowest growth rate (EVO4) it would take more than 100 years to achieve 1.3 m.

Mortality

The average five-year mortality rate was 17.0% for spruce, 40.9% for birch, and 33.9% for pine. It was negatively correlated with tree height for spruce and birch but not for pine (Figure 3). Correlations between mortality and tree height for spruce, birch and pine were −0.081 ($p < 0.0001$), -0.201 ($p < 0.0001$) and 0.066 ($p = 0.300$), respectively. Basal area and mortality were positively but rather weakly correlated for spruce ($r = 0.010$, $p = 0.050$), while the correlation was stronger for birch ($r = 0.128$, $p < 0.0001$) and pine ($r = 0.129$, $p = 0.041$). Mortality appeared to be higher during the second observation period when compared to the first period: the species-wise periodic rates for spruce, birch and pine were 15.9, 22.3 and 12.7%; 36.2, 41.7 and 44.9%; and 15.1, 45.7 and 41.0%, respectively. One explanation for the increase of mortality during the second period was that losses incurred in stand-specific selection cuttings were not possible to separate from natural
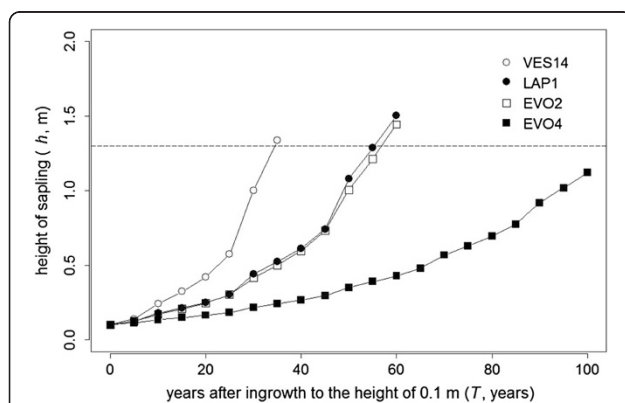
Figure 2 Predicted height developments (Equation 1) of initially 0.1 m tall spruces having an average growth potential. Stand-specific growth patterns were predicted for the experimental stands with highest (VES14), medium (LAP1 and EVO2) and lowest (EVO4) growth rates.
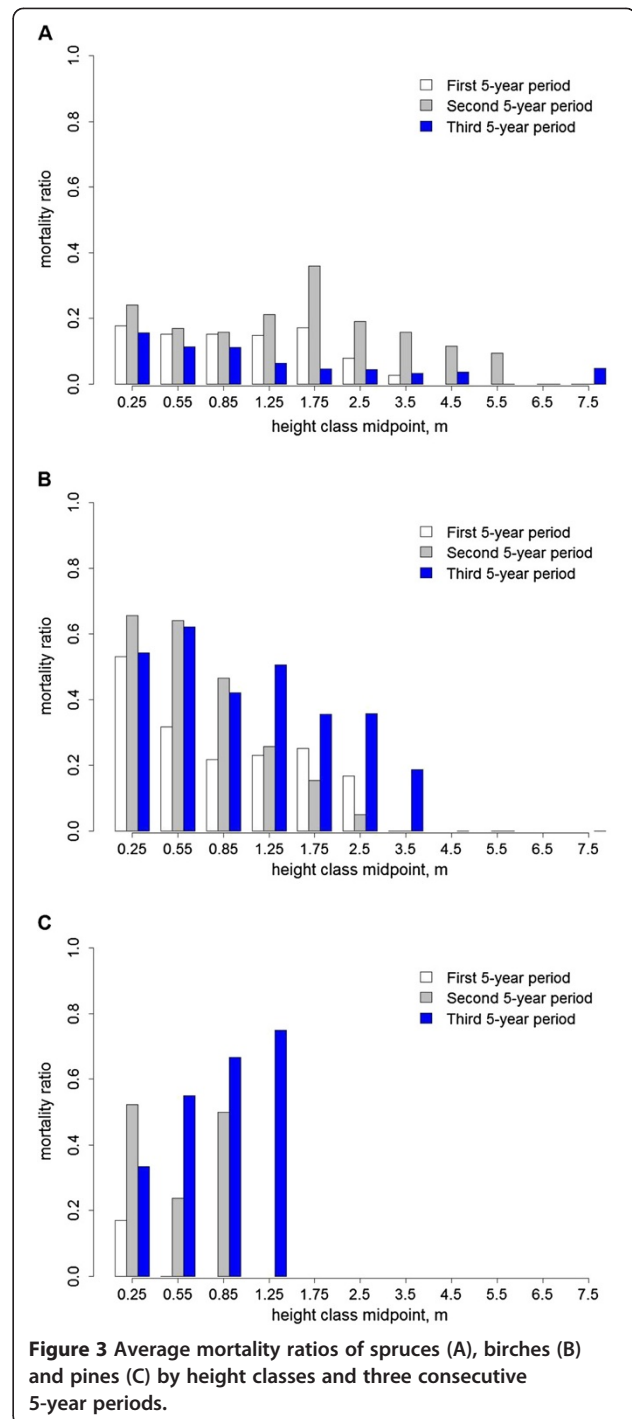
Figure 3 Average mortality ratios of spruces (A), birches (B) and pines (C) by height classes and three consecutive 5-year periods.

mortality. It is also noteworthy that the highest ratio of mortality for spruce was found in the height class 1.5–1.99 m during the second growth period.

Ingrowth

In this study, the ingrowth denotes the number of trees that reached the breast height of 1.3 m during any of the

three 5-year observation periods and survived until the last measurement. The mean annual ingrowth rates for spruce, birch and pine were 30.4, 2.8 and less than 0.1 trees per hectare, respectively. Variation between the periods and stands was remarkable, and correlations between ingrowth and basal area were very weak and nonsignificant for spruce ($r = -0.009$, *p*-value = 0.954) and birch ($r = -0.162$, *p*-value = 0.271), whereas for pine it became meaningless to estimate the correlation coefficient due to too few observations.

Height distributions

The height distribution of small spruces over the entire data at the beginning (1st measurement) and the end (4th measurement) of the 15-year monitoring period are shown in Figure 4A. The comparison calculations were only obtained for trees shorter than 4 m because taller trees were not measured at the beginning. Higher frequencies were obtained for the smallest height classes ($0.1 \le h < 1.05$ m), but the rest of the distribution had remained virtually unchanged. The pines and birches belonged mostly to the lowest height classes so that their height distributions seemed irrelevant for such comparisons.

Due to the simultaneous growth and mortality processes, the height distribution of spruces changed only little during the entire period of 15 years. The sizeable ingrowth rate in the three lowest height classes ($0.1 \le h \le 1.5$ m) of spruce obviously resulted from the very abundant regeneration cohorts of 1990 and 1993 (see Saksa and Valkonen, 2011). Ingrowth and mortality seemed to have cancelled each other out in higher height classes.

It is also noteworthy that the number of trees in the smallest height class decreased only in the case of two experimental stands (LAP1 and LAP7) from the first to the last measurement on the ERIKA plots (Figure 4B). If stand No. 7 in Lapinjärvi (LAP7) is not considered, all stands (VES13, VES16, EVO2, EVO3 and VEP5) with initially high number of small-sized trees retained their rank until the end of the monitoring period of 15-years.

Discussion

Lundqvist (1989) reported faster height growth with greater height of spruces (10–130 cm) in uneven-aged stands. In height class 10–40 cm, the average annual increment was about 2 cm and in the class of 100–130 cm it was about 5 cm. The annual height increment predictions obtained for the medium growth forests (LAP1 and EVO2 in Figure 2) and same size classes using Equation 1 were ca. 1 and 4 cm, respectively, which correspond to the findings of Lundqvist (1989). Nilson and Lundqvist (2001) also reported comparable results: average annual height increments of spruces ($h = 50–200$ cm) varied between 2–4 cm in a central Swedish

Figure 4 Height distributions of spruces with 0.1≤h<4 m at the beginning (1st measurement) and at the end (4th measurement) of the 15-year observation period are given in Figure A, whereas stand-specific numbers of trees in the smallest height class (0.1 ≤ h < 0.4 m) by experimental stands at the beginning and at the end of the 15-year observation period are indicted in Figure B.
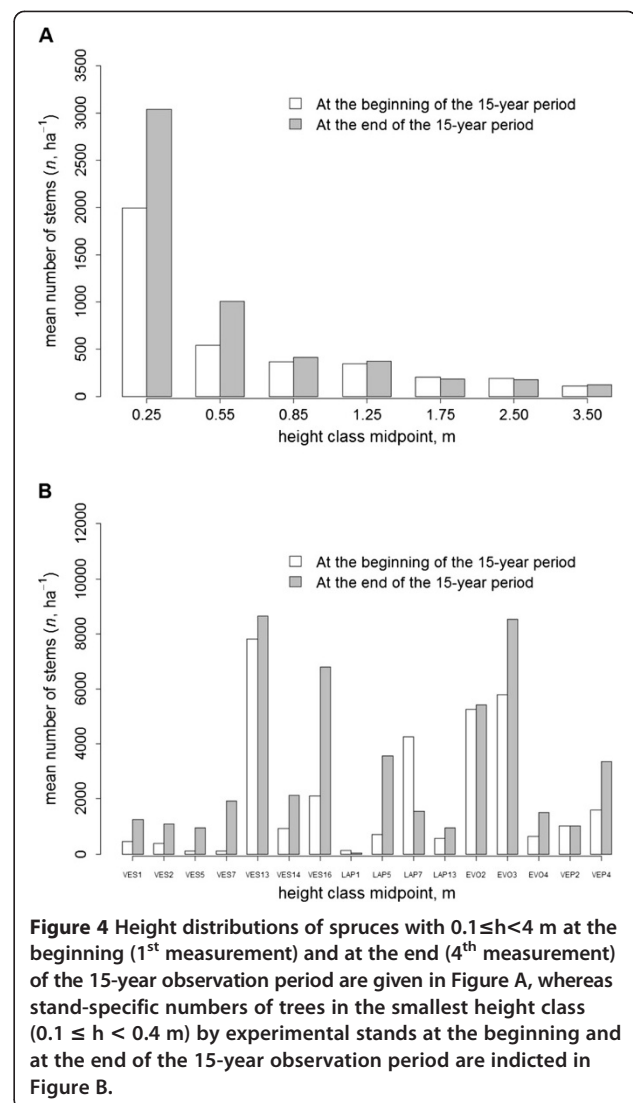
location before or a few years after thinning from above. Seven years after the thinning treatment, annual height increments had increased to 5–15 cm, and the highest average was obtained for the treatment called "medium overstorey density".

The nonlinear mixed-effects model on spruce height increment over height (Equation 1) is still too simplistic for use in simulation system applications. However, it serves the purpose of being a straightforward and unbiased analysis and demonstration tool for assessing the development of an average pattern observed in these experimental stands and supporting future efforts to construct operational models for simulation systems. The effects of complexity clearly apparent in these data shall be described in greater detail for simulation purposes. Then the true influence of stand density and its variation within stand on the growth and survival of trees needs to be analysed and modelled in order to obtain

statistically sound predictors required for simulation studies. However, even this preliminary exercise clearly revealed that the average growth of the small trees is slow in the ERIKA stands, especially in the smallest size classes. This corresponds closely to the recent findings by Saksa and Valkonen (2011): it took from 13 to 16 years for spruce germinants to grow into the height class of 15–30 cm in these same stands, and trees reached breast height at 60 years of age on average, and 5 m at 90 years, respectively. It is noteworthy that according to Lundqvist (1989) it took from 24 to 47 years for 0.1 m tall spruces in six different stands and corresponding conditions in central Sweden to reach breast height. Even if the tree growth rates in ERIKA stands were lower than those in Swedish selection cutting stands, the differences between stand-wise predicted mean growth rates were also substantial as demonstrated in Figure 2.

Stand basal area significantly reduced spruce height growth in the analysis conducted with the nonlinear mixed-effects model (Equation 1). Lundqvist (1989) and Lundqvist and Fridman (1996) did not detect any negative influence from high levels of standing volume on height increment, but it was also concluded that it was not possible to determine whether it would represent a general pattern or just a peculiarity of their dataset. Nilson and Lundqvist (2001) found that standing volume did have a negative correlation with the growth of small trees with thinning from below but not with thinning from above, i.e. in the case of stands with greater structural complexity. Chrimes and Nilson (2005) found a pronounced negative correlation between the growth of small trees with stand basal area or canopy openness at a subarctic location in Northern Sweden. Nilson (2001) and Chrimes and Nilson (2005) suggested that canopy openness, or light availability, could be more closely related to the growth of small trees than stemwood-based density attributes in such stands. Stemwood-based variables seemed to work better with increasing tree size as the role of root competition became more important. It seems likely that the acceleration of growth of small spruces during the monitoring years from 10 to 15 would be attributable to the selection cutting carried out at year 5. The pattern was similar as in the study of Nilson and Lundqvist (2001) who reported that stand density alone did not have a significant effect on increment, whereas cuttings (thinning from above or below) itself and the combined effect of cuttings and stand density influenced height increment significantly. It is expected, however, that local competition measures with spatiotemporal analysis could explain the variation in the growth characteristics of young trees in the structurally heterogeneous uneven-aged forest stands more profoundly (cf. Eerikäinen et al., 2007).

A total of 11 out of the 16 study stands were treated with a selection cutting after the 5th growth season. Theoretically, this could have resulted in different increment regimes between the two categories, but it was very unlikely though. Altogether three out of five uncut stands (VES13, VES14, and VES16) were left untouched because they had already been cut three years prior to the start of ERIKA monitoring. In the other two stands (LAP1, EVO3), 8 years had elapsed since the previous cutting, but tree growth had been too slow to facilitate (or necessitate) another cutting. A poorer site (a stony outcrop with shallow soil) combined with rather old dominant trees was the obvious reason for the slow growth rates of advanced trees at ERIKA plot called "EVO3". We could not identify any such distinct factors for LAP1 where the site fertility was definitely at least at average level. Consequently, we believe that all of the uncut stands were similar enough with the cut ones to be included in the data.

Indistinct background factors and interactions included in experimental conditions and data structure are probably involved. The short observation periods in the studies (≤ 15 years) are certainly part of the issue, because the response of understorey spruce trees to harvesting treatments is slow. Typically it takes several years for heavily suppressed spruces to show any positive growth response, and more than 10 years to attain full growth after complete release, i.e. removal of overstorey (Koistinen and Valkonen, 1993; Nilson and Lundqvist, 2001).

For birch and pine, the relationship between tree growth and height was not nearly as consistent as it was for spruce. One explanation could be that their data was patchy due to the limited presence of the two species in the experimental ERIKA stands. Perhaps more importantly, their initially quite good growth rate did not accelerate with height at all like it did in the case of spruce. Both of these two patterns point to the same basic feature which is the inability of birch and pine to survive and grow under dense spruce main canopies.

Mortality estimates were obtained for trees that had existed at a particular measurement but died or went missing five years later. The results underestimated true mortality rates for the smallest height class by failing to capture trees that grew in to the class and then died between measurements, not leaving a mark in the records. Conversely, estimates for the second period (1996–2001) included losses incurred in logging. Since trees were not remeasured after harvesting, it was not possible to make any distinction between their disappearance due to logging or due to other reasons. The proportion of trees lost in logging seemed to be relatively low in this dataset. The total loss rate (died or vanished during the period) of spruce obtained for the second period was higher when compared to the first and third period, whereas an

increasing rate of loss was obtained for birch. The data for pine was too erratic for more complete conclusions. Under comparable circumstances, a logging entry can cause death or injury from 30 to 40% of small spruces (Granhus and Fjeld, 2001; Surakka and Sirén, 2007; Surakka et al., 2011). Nilson and Lundqvist (2001) observed that annual mortality rates of spruces (0.1 m $\leq h < 0.5$ m and 0.5 m $\leq h < 2.0$ m) varied from 2 to 7% and from 0 to 4%, respectively. In the data of this study, the annual mortality rates were from the same magnitude, i.e. 3.7% and 3.1%, when obtained for the corresponding height classes of spruces, respectively.

Lundqvist (1989, 1991, 1993) estimated that with the threshold height of 1.3 m an average annual spruce ingrowth varied from 43 to 55 ha^{-1}, whereas Saksa (2004) found it to be 26 ha^{-1}. Both data were characterised by a high variability in stand density. In central Sweden, Lundqvist et al. (2007) observed an annual ingrowth rate of 21 spruces per hectare with the threshold of 5 cm at breast height, which was a lump average for plots treated with light to heavy thinning from below or above. Correlation with standing volume was significantly negative. It is essential to understand that short-term ingrowth is largely a function of the initial size distribution of trees, while stand density should have a more meaningful impact over a longer period. Such is also the case in this study, and the observed ingrowth rates must be interpreted accordingly.

As the product of the growth and mortality processes, the height distribution of small spruces was little changed during the 15 years in ERIKA plots. The sizeable ingrowth rate in the lowest height classes ($0.1 \leq h \leq 0.7$ m) of spruce obviously resulted from the very abundant regeneration cohorts of 1990 and 1993 (see Saksa and Valkonen, 2011). Ingrowth and mortality seemed to have cancelled each other out in higher height classes. As reported by Saksa and Valkonen (2011), the experimental ERIKA stands have a good regeneration potential on average, and quite a few spruces are about to reach 1.3 m in height because of the two abundant cohorts emerged in the early 1990s.

In addition to tree survival, growth, and momentary ingrowth rate, their long-term dynamic is controlled by developments at the consecutive stages of their development. However, the very large variations within and between stands suggest that problems may surface in many cases. More intensive harvestings (i.e., lower post-harvest stand densities) than those implemented in the ERIKA stands could be applied to enhance the survival and growth of small spruces, but their true impacts remain uncertain. It is also obvious that the shade intolerant species such as birch and pine cannot develop into serviceable undergrowth, let alone full-fledged trees, in these spruce-dominated selection stands with relatively high stand density levels. More intensive management including much heavier thinning programs or group selection practices would be required to sustain their participation in the uneven-aged spruce-dominated forest stands.

Conclusion

In conclusion, the performed analyses inspected and demonstrated some of the major elements of the dynamics among small trees in the uneven-aged spruce forest stands. The height increment model for spruce is simplistic for use in simulation systems but supports our future efforts to construct operational model systems. The inherent complexity of the phenomena involved became clearly apparent. To reveal the true influence of stand density and its within-stand variation on the growth and survival of small trees is of particular importance for practical needs and simulation purposes. Many of our empirical results are very well in line with their counterparts in the Nordic area. This reinforces our understanding that it would be possible and very beneficial to compound our rather patchy data sets for comparison, testing and modelling.

Author details
[1]Finnish Forest Research Institute, Joensuu Unit, P.O. Box 68, FI-80101 Joensuu, Finland. [2]Finnish Forest Research Institute, Vantaa Unit, P.O. Box 18, FI-01301 Vantaa, Finland. [3]Finnish Forest Research Institute, Suonenjoki Unit, Juntintie 154, FI-77600 Suonenjoki, Finland.

References
Andreassen K, Öyen B (2002) Economic consequences of three silvicultural methods in uneven-aged mature coastal spruce forests of central Norway. Forestry 75:483–488

Cajander A (1926) The theory of forest types. Acta Forestalia Fennica 29(3):1–108

Chantal MD, Leinonen K, Kuuluvainen T, Cescatti A (2003) Early response of Pinus sylvestris and Picea abies seedlings to an experimental canopy gap in a boreal spruce forest. For Ecol Manag 173:321–336

Chrimes D, Nilson K (2005) Overstorey density influence on the height of Picea abies regeneration in northern Sweden. Forestry 78(4):433–442

Clarke G (1992) The natural regeneration of spruce. Scott For 6(2):107–129

Eerikäinen K, Miina J, Valkonen S (2007) Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. For Ecol Manag 242:444–461

Fjeld D (1998) Injuries after selection harvesting in multi-storied spruce stands – the influence of operating systems and harvest intensity. Journal of Forest Engineering 9(2):33–40

Gobakken T, Lexerød N, Eid T (2008) T: A forest simulator for bioeconomic analyses based on models for individual trees. Scand J For Res 23(3):250–265

Goldstein H (1995) Multilevel statistical models, 2nd edn. Arnold, London, 178 p

Granhus A (2001) Partial cutting in Norway spruce: impacts on advance regeneration and residual stand, Doctor Scientiarum theses 13. Agricultural University of Norway, Ås, Norway, 34 p. + app0

Granhus A, Fjeld D (2001) Spatial distribution of injuries to Norway spruce advance growth after selection harvesting. Can J For Res 31:1903–1913

Hanssen K (2002) Effects of seedbed substrates on regeneration of *Picea abies* from seeds. Scand J For Res 17:511–521

Hanssen K (2003) Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. For Ecol Manag 180:199–213

Hanssen K, Granhus A, Brække FH, Haveraaen O (2003) Performance of sown and naturally regenerated *Picea abies* seedlings under different scarification and harvesting regimens. Scand J For Res 18(4):351–361

Koistinen E, Valkonen S (1993) Models for height development of Norway spruce and Scots pine advance growth after release in southern Finland. Silva Fennica 27(3):179–194

Kolström T (1993) Modelling the development of an uneven-aged stand of *Picea abies*. Scand J For Res 8(3):373–383

Lexerød N (2005) Recruitment models for different tree species in Norway. For Ecol Manag 206:91–108

Lexerød N (2008) Economic efficiency of selective cutting under different timber price scenarios, Philosophiae Doctor (PhD) Thesis 36. Norwegian University of Life Sciences, Ås, Norway, p 31 p

Lundqvist L (1989) Blädning i granskog - strukturförändringar, volymtillväxt, inväxning och föryngring på försöksytor skötta med stamvis blädning [Use of the selection system in Norway spruce forests - changes in stand structure, volume increment, ingrowth and regeneration on experimental plots managed with single-tree selection]. Ph D. Thesis. Swedish University of Agricultural Sciences, Institute of Silviculture, Umeå, p 22, + 4 appendix papers. (In Swedish.)

Lundqvist L (1991) Some notes on the regeneration of Norway spruce on six permanent plots managed with single-tree selection. For Ecol Manag 46:49–57

Lundqvist L (1993) Changes in the stand structure on permanent *Picea abies* plots managed with single-tree selection. Scand J For Res 8:510–517

Lundqvist L (1995) Simulation of sapling population dynamics in uneven-aged *Picea abies* forests. Ann Bot 76:371–380

Lundqvist L, Fridman E (1996) Influence of local stand basal area on density and growth of regeneration in uneven-aged *Picea abies* stands. Scand J For Res 11:364–369

Lundqvist L, Chrimes D, Elfving B, Mörling T, Valinger E (2007) Stand development after different thinnings in two uneven-aged *Picea abies* forests in Sweden. For Ecol Manag 238:141–146

Miina J, Eerikäinen K, Hasenauer H (2006) Forest Management – modeling forest regeneration. In: Hasenauer H (ed) Sustainable Forest Management – Growth models for Europe. Springer Verlag, Berlin, pp 93–109

Nilson K (2001) Regeneration dynamics in uneven-aged Norway spruce forests with special emphasis on single-tree selection. Acta Universitatis Agriculturae Suecica Silvestria, Umeå, Sweden, 209: 25 p. + 4 appendix papers

Nilson K, Lundqvist L (2001) Effect of stand structure and density on development of natural regeneration in two *Picea abies* stands in Sweden. Scand J For Res 16:253–259

Örlander G, Karlsson K (2000) Influence of shelterwood density on survival and height increment of *Picea abies* advance growth. Scand J For Res 15:20–29

Pinheiro JC, Bates DM (2002) Mixed-Effects Models in S and S-PLUS. Corrected third printing. Springer-Verlag, New York, p 528

Pukkala T, Kolström T (1992) A stochastic spatial regeneration model for *Pinus sylvestris*. Scand J For Res 7:377–385

Pukkala T, Lähde E, Laiho O (2009) Growth and yield models for uneven-sized forest stands in Finland. For Ecol Manag 258:207–216

Pukkala T, Lähde E, Laiho O (2010) Optimizing the structure and management of uneven-sized stands of Finland. Forestry 83(2):129–142

Saksa T (2004) Regeneration process from seed crop to saplings – a case study in uneven-aged Norway spruce-dominated stands in Southern Finland. Silva Fennica 38(4):371–381

Saksa T, Valkonen S (2011) Dynamics of seedling establishment and survival in uneven-aged boreal forests. For Ecol Manag 261(8):1409–1414

Surakka H, Sirén M (2007) Poimintahakkuiden puunkorjuun nykytietämys ja tutkimustarpeet. [Review on harvesting techniques in selection silviculture including research priorities]. Metsätieteen aikakauskirja 4:373–390, In Finnish

Surakka H, Sirén M, Heikkinen J, Valkonen S (2011) Damage to saplings in mechanized selection cutting in uneven-aged Norway spruce stands. Scand J For Res 26(3):323–244

Tahvonen O (2009) Optimal choice between even- and uneven-aged forestry. Nat Resour Model 22(2):289–321

Tahvonen O, Pukkala T, Laiho O, Lähde E, Niinimäki S (2010) Optimal management of uneven-aged Norway spruce stands. For Ecol Manag 260:106–115

Team Core (2012) R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing, ISBN 3-900051-07-0, URL http://www.R-project.org/

Valkonen S, Maguire D (2005) Relationship between seedbed properties and the emergence of spruce germinants in recently cut Norway spruce selection stands in Southern Finland. For Ecol Manag 210:255–266

Wikström P (2000) A solution method for uneven-aged management applied to Norway spruce. For Sci 46(3):452–463

Wikström P (2008) Jämförelse av ekonomi och produktion mellan trakthyggesbruk och blädning i skiktad granskog - analyser på beståndsnivå baserade på simulering. [Economics and yield in spruce stands with complex structures with even-aged and uneven-aged management – analyses at stand level based on simulation]. Skogsstyrelsens rapport 24:48, In Swedish