Eesti Maaülikool
Estonian University of Life Sciences

GROWTH OF ADVANCE REGENERATION OF NORWAY SPRUCE AFTER CLEARCUT

HARILIKU KUUSE EELUUENDUSE KASV LAGERAIE JÄRGSELT

MAREK METSLAID

A Thesis
for applying for the degree of Doctor of Philosophy in Forestry

Väitekiri
filosoofiadoktori kraadi taotlemiseks metsanduse erialal

Tartu 2008

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, references to which in the text are by their Roman numerals.

I **Metslaid, M.**, Jõgiste, K., Nikinmaa, E., Moser, W.K., Porcar-Castell, A. 2007. Tree variables indicating the growth response and acclimation of advance regeneration of Norway spruce and other coniferous species after the release. Forest Ecology and Management 250, 56-63.

II Jõgiste, K., **Metslaid, M.** 2002. Acclimation of spruce advance regeneration to light conditions: estimation by needle characteristics. Forestry Studies / Metsanduslikud uurimused 36, 26-31.

III **Metslaid, M.**, Ilisson, T., Nikinmaa, E., Kusmin, J., Jõgiste, K. 2005. The recovery of advance regeneration after disturbances: acclimation of needle characteristics in *Picea abies*. Scandinavian Journal of Forest Research 20 (Suppl. 6), 112-121.

IV **Metslaid, M.**, Ilisson, T., Vicente, M., Nikinmaa, E., Jõgiste, K. 2005. Growth of advance regeneration of Norway spruce after clear-cutting. Tree Physiology 25, 793-801.

The contributions of the authors to the papers were as follows:

	I	II	III	IV
Original idea	MM	KJ	KJ, MM, EN	KJ, MM
Study design	MM, EN	KJ, MM	KJ, MM	KJ, MM
Data collection	MM	MM, KJ	MM, TI	MM, MV, TI
Data analysis	MM, APC	KJ, MM	MM, EN	MM, MV, EN, KJ
Manuscript preparation	MM, KJ, EN, WKM, APC	KJ, MM	MM, TI, KJ, EN, JK	MM, TI, KJ, EN, MV

APC – Albert Porcar-Castell; EN – Eero Nikinmaa; JK – Jürgen Kusmin; KJ – Kalev Jõgiste; MM – Marek Metslaid; MV – Marta Vicente; TI – Triin Ilisson; WKM – W. Keith Moser

ABBREVIATIONS

H	Tree height, cm
D	Tree diameter at root collar, cm
LCB	Living crown base, cm
CD	Crown diameter, cm
TL	Top shoot length, cm
L	Length of shoot, cm
M	Needle mass of shoot, g
N	No. of needles
V	Needle volume of shoot, mm^3
I	Diameter increment (at ground level), mm $year^{-1}$
G	Tree basal area (at ground level), mm^2
Ig	Tree basal area increment (at ground level), mm^2 $year^{-1}$
K	Competition index

1. INTRODUCTION

Modern forestry has been evolving towards multiple use of forests and maintenance of biodiversity. Interest in integrating natural forest dynamics into management planning and silvicultural practices has increased as a result of concern over biodiversity values and maintaining ecological functions in managed forests. Natural regeneration is attracting more interest because of environmental concerns, since biodiversity, wildlife habitat preservation, and recreation are increasingly important goals of ecosystem management. Promoting the establishment and growth of advance regeneration offers several advantages. Advance regeneration that responds to release with increased height and diameter growth provides immediate stocking, shade for subsequent seedlings, an aesthetically pleasing landscape, protective cover for wildlife, and soil protection. Furthermore, the use of advance regeneration reduces rotation length and silvicultural cost (Ruel et al., 2000; Ferguson and Adams, 1980; Lähde et al., 1999; Jeansson et al., 1989). Advance regeneration improves the chances of local genetic pool survival and conservation.

Stand-levelling windstorms and clear-cut logging often leave advance regeneration of varying size and age distribution in place (Frelich, 2002; Abaturov and Melanholin, 2004). The growth of saplings can be modelled after artificial regeneration (Braathe, 1988; Nyström and Kexi, 1997; Valkonen, 1997; Sikström, 2004) or for advance regeneration (Coates, 2000; Wright et al., 2000). The biggest difference between advance regeneration and seedlings introduced to the site via artificial regeneration is their size distribution and spacing. Spacing of advance regeneration is sometimes very dense, because understorey saplings often occur in patches that have established themselves in previous canopy openings. It is therefore important to know the external attributes of trees, based on what it would be possible to make decisions in selecting future trees. The trivial answer would concern the tree size, but there is also a need to find some other visual characteristics (factors) which would help to identify the most viable trees (future crop trees) in these dense patches. The planted seedlings are of similar size and their above-ground portion has become acclimated to open-growth conditions in the nursery. Stress from transplanting and new soil conditions, however, can have a considerable negative effect on growth (see Kauppi, 1984). Although natural advance regeneration does not suffer from planting stress, seedlings and saplings are subjected to very different growth conditions after forest clearing from those in their original environment. In response, advance regeneration shows considerable reallocation of resources between shoots and roots (Kneeshaw et al., 2002). Sapling size before stand opening impacts the time it takes for the saplings to adjust to the new growth conditions (Kneeshaw et al., 2002).

According to the Estonian Forest Act, several cutting systems are permitted in forest management. Regeneration cutting, divided into clear-cutting and shelterwood cutting, is permitted for forest regeneration or reforestation. In clear-cutting, all trees are removed from the cutting area within a year of the start of cutting, with the exception of 20-70 scattered seed trees per hectare and vigorous advance regeneration (undergrowth), retention trees, and trees for biodiversity. Shelterwood cutting is divided into uniform shelterwood cutting, group-selection cutting and shelterwood strip cutting. In uniform shelterwood cutting, the forest subjected to reforestation should be cut by dispersed single trees in several cutting stages over ten to twenty years. In the case of group-selection cutting, the forest earmarked for reforestation should be cut by groups in several cutting stages over twenty to forty years. In the shelterwood strip cutting, the forest subject to reforestation should be clear-cut from the cutting area edges, from other places scattered single trees or gaps in several cutting stages over twenty to forty years.

An understanding of sapling growth and mortality is fundamental to predicting forest successional dynamics and for prediction of forest regeneration in managed stands after partial or complete release of advance regeneration (Wright et al., 2000). Numerous variables have been tested to explain the mortality and growth of advance regeneration after release. The most frequently suggested attributes are height, age, live crown ratio, and height or diameter growth before harvest (Ruel et al., 1995; Örlander and Karlsson, 2000). Previous growth and the growth tendencies of the tree have been used in empirical individual-tree growth models to predict subsequent growth (Pukkala and Kolström, 1991). However, needle morphology and crown architecture also can characterize relative growth and acclimation to new conditions (Sellin, 2001b; Parent and Messier, 1995; Reich et al., 1998). Combining these structural characteristics with tree physiology may allow the development of predictive tools that would facilitate derivation of practical recommendations for the management of advance regeneration. Forest managers can emulate disturbance patterns in their forest management decisions as they learn more about the success of particular species in regenerating after disturbance (Fujimori, 2001; Jõgiste et al., 2005).

Needle-mass variables have been related to growth and acclimation as relative or absolute values. Reich et al. (1998) demonstrated tree acclimation to shading based on relative morphological variables, needle morphology being strongly correlated with variation in relative growth rate. Previous tree growth can be used as an attribute for growth projection in empirical individual-tree growth models (as in Pukkala and Kolström, 1991). Although increment data from tree rings or repeated measurements reflect the growth conditions and history, there is much unexplained variation in currently available models of advance regeneration because of the many factors that affect it.

Norway spruce (*Picea abies* (L.) Karst.) is a shade-tolerant tree species which can produce a viable population of advance regeneration that can exist for long periods beneath the canopy of a mature forest stand (Jeansson et al., 1989; Lundqvist and Fridman, 1996; Valkonen et al., 1998). Advance growth of Norway spruce and other species can be utilized for forest regeneration (Greene et al., 2002; Kuuluvainen, 2002). Forestry practices in Estonia recommend saving advance regeneration during forestry operations such as logging. However, little is known about how such released trees acclimate to the new environmental conditions or their subsequent growth performance. Furthermore, a scientific basis for developing procedures for tending dense regeneration groups following release is lacking, because the characteristics that could serve as reliable indicators of the performance of advance regeneration trees forming the next generation after clear-cutting have not been identified and the factors controlling the performance of such trees after clear-cutting have not been well defined.

2. REVIEW OF LITERATURE

Since the forestry literature has been reviewed in paper **I**, the following section presents a review of selected literature about the growth response and acclimation of advance regeneration of Norway spruce after release (clear-cut).

The canopy of the forest stand, which may be of various densities, influences the light conditions (light availability) in the understorey. The amount of light received by the understorey is an important factor for seedling establishment, survival and growth (Lieffers et al., 1999). In general, at least 20 percent of full sunlight is required for survival over a period of years (Barnes et al., 1998). Norway spruce is one of the shade-tolerant tree species producing advance regeneration. The natural death of an individual tree or a group of trees or windthrow in the forest stand creates a canopy opening (canopy gap) that favours the establishment of natural regeneration and the existing advance regeneration (Hytteborn et al., 1987; Leemans, 1991). Norway spruce is one of the most common tree species in gap refilling (Liu and Hytteborn, 1991; Drobyshev, 1999). Gaps are also generated by silvicultural systems, which remove the dominant trees (Coates and Burton, 1997). At the same time canopy gaps may be of various sizes and positions (Liu and Hytteborn, 1991; Coates, 2000; Coates, 2002). It is also possible to construct the canopy structure (situation) based on the number of stumps, when light is not measured under the old canopy.

Since advance regeneration after disturbance depends on the properties of the forest environment prior to disturbance and the type of disturbance (Tesch and Korpela, 1993; Man'ko, 1967; 2005), several models that include different site factors have been developed to model the growth of advance regeneration of Norway spruce (e.g., Valkonen, 1997). For example, seedbed characteristics (Kneeshaw and Bergeron, 1996; Lieffers et al., 1996; Rooney and Waller, 1998; Cornett et al., 2001; Hanssen, 2003) and soil water conditions have been investigated (Brang, 1998; Sellin, 2001a; Kneeshaw et al., 2002, Nilsson et al., 2002). The survival of the saplings established under the canopy, however, depends on the available light and current growth rate (Coates, 2002; Claveau et al., 2002; Kobe and Coates, 1997). The role of competition after cutting is very important (Kneeshaw and Bergeron, 1996; Hanssen, 2003; Nilson and Lundqvist, 2001; Duchesneau et al., 2001; Tesch et al., 1993; Grassi and Giannini, 2005). The acclimation response reflects growth performance prior to release, which in turn reflects pre-release environmental conditions.

Changes in growth allocation in different parts of the tree in combination with altered soil and light conditions strongly influence tree growth response following release (Kneeshaw et al., 2002; Claveau et al., 2002). The secondary (diameter) growth of a tree may occur several years after the release (Youngblood, 1991). Kneeshaw et al. (2002) found that height growth does not respond immediately after release, growth reaction being seen first in the roots. The same authors reported that changes in allocation patterns from above-ground to below-ground tissues might vary with climate and the degree of overstorey removal. These findings are in agreement with the suggestion that trees try to maintain the balance between their crown (above ground) and root system (below ground) functions (Nikinmaa, 1992). As relative growth rate and size increases, wood as against leaf allocation starts to become a more important determinant of the sapling performance (Mäkelä, 1988; Nikinmaa et al., 2003).

Silviculture based on the dynamics and structure of natural forests is called nature-oriented, ecologically oriented, or close-to-nature. Single-tree or group-selection harvests emulate the small-size gap disturbance that has been suggested as an important regeneration mechanism, for example, in natural Norway spruce forests of Northern Europe (Kuuluvainen, 2002). Selection cutting focuses on individual trees or groups of trees, and seed-tree or shelterwood cutting systems operate at the stand level in diversity-oriented silviculture (Lähde, 1992; Lähde et al., 1999). The selection system aims at stand structures that consist of seedlings and trees of all ages, the objective being to cut both large and small trees (Jeansson et al., 1989). Trees removed in single-tree selection are replaced by natural advance regeneration (Lundqvist and Fridman, 1996; Dobrowolska, 1998). The use of advance regeneration is not limited to selection cutting systems; where even-aged systems such as clear-cutting or shelterwood cutting, are used, advance regeneration can be relied on if care is taken to protect the saplings during the logging operation.

RESEARCH NEEDS

Although increment data from tree rings or repeated measurements reflect the growth conditions and history because of many factors that affect advance regeneration, there is much unexplained variation in currently available models. The model developed in this study has qualitative application value, and forestry practitioners can use its diagnostic capacity to predict the regeneration success of various size classes. However, the model cannot be used for extrapolations, because it has not yet run for canopy trees or for periods longer than 5-6 years after clear-cutting.

Combining structural characteristics with plant physiology may allow the development of predictive tools that would facilitate derivation of practical recommendations for the management of advance regeneration. As forest managers learn more about species success in regenerating after disturbances they can emulate disturbance patterns in forest management decisions (Fujimori, 2001; Jõgiste et al., 2005).

Stand-level variables can be obtained from individual tree measurements. However, a physiological mechanism must be used to interpret the data in the present work. Process-based models can provide a basis for the explanation of the present results (Hari et al., 1985) (**II**). The link between morphological changes and real growth in the future provides useful estimation tools for practising foresters.

At the moment, the new method has been applied (developed) to use eco-physiological variables for modelling advance regeneration. Gas exchange is mainly measured in new shoots of advance regeneration trees using, the portable photosynthesis system CIRAS-1 (PP Systems) for this purpose. The photosynthesis variables measured describe the growth dynamics of young trees directly. The photosynthetic capacity of the shoots is the direct indicator of tree acclimation in new conditions.

The replanting of advance regeneration to controlled conditions is one of the challenges and is planned for future activity. Measuring gas exchange with the CIRAS-1 portable photosynthesis system is planned.

The challenge for forestry practice is to develop new regeneration methods which enable a combination of natural and artificial regeneration.

3. AIMS OF THE STUDY

Norway spruce is the only species in boreal Europe with characteristics that allow the use of advance regeneration in its silviculture. However, efficient use of advance regeneration requires knowledge of the factors influencing its performance. The particular questions of interest are how Norway spruce acclimates to understorey conditions and subsequent release, and how these features could be used to predict sapling performance after release. This work is a continuation of my M. Sc. thesis (Metslaid, 2004).

The aims of the present doctoral thesis were:

1. To review selected literature on the relationships between different tree variables and ecophysiological factors that influence the growth response and acclimation of Norway spruce advance regeneration to release (**I**);
2. To see how Norway spruce acclimates to understorey conditions and subsequent release, and how these features could be used to predict the sapling performance after release (**I**);
3. To see whether needle mass characteristics of trees can be related to growth data and to develop a basal area growth model for recovery of advance regeneration of Norway spruce trees after clear-cutting (**II, IV**);
4. To determine whether shoot and needle properties describe the dynamics of Norway spruce response to a clear-cut that exposes them to full sunlight (**III**).

4. MATERIALS AND METHODS

4.1. Study areas

Järvselja, situated in the south-eastern part of Estonia (58° 25′ N, 27° 46′ E) in Tartu county near Lake Peipsi, is situated in a temperate zone with a moderately cool and moist climate. The average annual temperature is 4 - 6°C. The annual precipitation is between 500 mm and 750 mm, of which about 40-80 mm falls as snow. The active period of vegetation growth (daily air temperature above 5°C) mostly lasts between 170 and 180 days per year.

The recovery (acclimation) of advance regeneration of Norway spruce trees was studied in four permanent sample plots located on sandy soils.

The first plot (1) was established on a 2.5-ha clearfelled area harvested during the winter of 1995/1996. The site type is *Oxalis-Myrtillus* (Lõhmus, 1984) and the site index is bonitet 1. Before felling, the stand consisted of 70% Norway spruce (*Picea abies* (L.) Karst.), 20% silver birch (*Betula pendula* Roth) and 10% trembling aspen (*Populus tremula* L.). The volume of the stand before clear-cutting (determined by basal area on all plots) was 338 m^3/ha^{-1}. Stand structure was uneven, and there were some gaps in the canopy. The advance regeneration was not distributed evenly over the clear-cut area. Trees were sampled in two patches 40 m apart, a dense group under previously heavy shade and a second patch that was in a canopy gap.

The second plot (2) was established on a 1.1 ha clearfelled area harvested during the winter of 1999/2000. The site type is *Oxalis-Myrtillus* (Lõhmus, 1984) and the site index is bonitet 1. The main canopy consisted of 90% Norway spruce, Scots pine (*Pinus sylvestris* L.) making up the balance. The volume of the stand before clear-cutting was 288 m^3/ha^{-1}. Most of the advance regeneration trees were located in one large group, but 15 trees were distributed separately in a second group.

The third plot (3) is a 0.6 ha stand situated next to the first, but beneath a dense canopy cover. The site index is bonitet 1 and the site type is *Oxalis-Myrtillus* (Lõhmus, 1984). The old canopy comprised 60% of Norway spruce, 30% of trembling aspen and 10% of silver birch. The volume of the stand is 329 m^3/ha^{-1}. The advance regeneration trees of various heights were unevenly distributed in large and small clumps. The overstorey of the stand has not been removed, but clear-felling was scheduled for winter 2007/2008.

The fourth plot (4) was established on a clearfelled area cut in winter 2001/2002. The size of the clear-cut was 2.1 ha. The site type is *Myrtillus* (Lõhmus, 1984) and the site index is bonitet 3. The old canopy comprised 65% Norway spruce, 30% silver birch, and 5% Scots pine. The volume of the stand before clear-cutting was 287 m^3/ha^{-1}. Most of the advance regeneration trees were located in one large group. There were trees in various height classes.

Plot size and configuration varied; the plot size was adjusted to accommodate 100 trees of various sizes and competition status. Because the density and tree size varied, plot size and shape were not fixed. Plots were centred on the groups of advance regeneration trees. All trees within the plot perimeter were measured to include competition effects, but if a group exceeded 100 trees, only a sub-area was sampled. In this case, the trees neighbouring sample trees, even though they fell outside the sample plot, but were within a 2-m radius of the sampled trees, were also measured. If the group was too small to include 100 trees, additional trees were selected, which explains why there were some separate groups. The trees were tagged with numbered metal labels and the stem locations mapped. The number of trees on plots included in the final analysis varied, depending on how many trees survived until the end of observation period.

In addition, coordinates were determined for advance regeneration other than Norway spruce, which was within a 2-m radius around the sample tree. These were trees taken into account in calculating the competition index.

4.2. Field and laboratory measurements

Measurements on advance regeneration trees were made at the end of each growing season and included tree height, diameter at the root collar, living crown base and crown diameter in two directions (the widest and the direction perpendicular to it). The height of the first living branch of the stem was considered equivalent to the crown base. In addition, the length of the top shoot (leader) was recorded.

At each measurement, a lateral shoot was sampled randomly from the upper third of each tree crown. Visual criteria were applied to ensure that no damaged shoots or any with extreme growth were included in the sampling (shoots with signs of browsing were excluded). This shoot from the upper third of the crown was always compared with a similarly selected shoot from the same tree from the previous year. The shoots and needles collected were assumed to reflect the growth capacity of the tree during the previous year. Excised shoots were taken to the laboratory where shoot length was measured and the number of needles counted. Needles were dried at 70°C for 72 h and weighed. Five randomly selected needles were measured for volume determination. The needle length, thickness and width were measured and the volume was calculated by the formula:

$$V = l * w * t * k \tag{1}$$

where l is needle length, w is needle width, t is needle thickness and k is a coefficient. The value of k was 0.8 (**II**). The mean of the five volumes was calculated and entered into the database as a shoot descriptor. Subtracting the current year's shoot from the needle mass of the previous year compared the shoots of different years. This value can be interpreted as a growth indicator, positive values indicating an increase in average shoot mass over the years.

Trees on plot 1 were sampled destructively after five years' growth in full light conditions. Basal discs were removed and tree rings were measured using WINDENDRO (Regent Instruments) (the width of each growth ring was measured and averaged from two radii).

4.3. Data analysis

The index of competition was calculated for each tree:

$$K = \sum_{K=1}^{N} \left(\frac{H_k}{H_k} * \frac{1}{S_k} \right) \tag{2}$$

where K is index of competition, H_k is the height of the competitor tree, H_0 is height of the tree and S_k is the distance from the competing tree (Hegyi, 1974). Some trees died during the observation period and this data is excluded from the analysis.

MS Excel (Microsoft, Redmond, WA), STATGRAPH (Version 5.0; STSC) and SAS software (version 8.0; SAS Institute, Cary, NC) were used for all correlation and regression analyses (**III-IV**). Correlation analysis was used to describe relationships between needle and shoot variables and the diameter increment, correlation matrixes being constructed to describe relationships between shoot variables of the same and consecutive years. Analysis of variance determined the relationships between the morphometric attributes of the trees (**III**). Growth dependencies over the years were subjected to simple regression analysis. Regression equations were fitted for different combinations of variables to obtain the best growth predictions. Tree increment was related to the previous increment and needle mass. The general linear model (GLM) procedure of SAS software was applied to study the relationships between variables (**III**). The effects of tree size and competition on growth, with increment and height class as the two factors, were evaluated by two-way analysis of variance (ANOVA) (**IV**). Four different regressors (M_t – shoot needle mass, I_t – diameter increment, N_t – number of needles, and L_t – shoot length) predicting needle mass growth of next year (M_{t+1}) were tested (**III**). Data from the plots were combined to produce the series for time elapsed since release from the old canopy (years 0–5). For these modelling attempts, the plot combinations were arranged as presented in Table 1 to show how the growth data from several plots were combined. Plots 1-3 were used in the analysis. Multiple regression analysis involving transformation of variables was used to describe relationships between tree size and growth in consecutive years, the aim being to predict basal area increment after clear-cutting on the basis of needle and tree characteristics (**IV**).

Table 1. Combination of plot data to demonstrate acclimation processes (years are indicated according to acclimation time and plot no.). Year indicates the observation year (i.e., the previous year was also covered by the data) (**III-IV**).

Plot	**Year after clear-cut**					
	0	**1**	**2**	**3**	**4**	**5**
1	-	1996	1997	1998	1999	2000
2	-	-	2001	2002	2003	-
3	2003	-	-	-	-	-

Note: year in the table indicates the observation year; the previous year was also covered by the data.

The following regression model was fitted to predict the needle mass of the next year (**III**):

$$\ln(M_{t+1})=a_0+a_1*\ln(M_t)+a_2*L_t \tag{3}$$

where M is the needle mass of a shoot from the upper third of the tree crown (g), L is the length of the shoot (cm) and t the time period (years).

The regression model was fitted for the increment function (n = 457, R^2 = 0.81, RMSE = 0.70) (**IV**):

$$\mathbf{In}\boldsymbol{I}_{g\,(t+1)} = \boldsymbol{a}_0 + \boldsymbol{a}_1 \mathbf{ln}\, \boldsymbol{I}_{g\,(t)} + \boldsymbol{a}_2 \boldsymbol{K}_t + \boldsymbol{a}_3 \mathbf{ln} \boldsymbol{G}_t + \boldsymbol{a}_4 \mathbf{ln} \boldsymbol{M}_t \tag{4}$$

where I_g is basal area increment, K_t is competition index at time t, G is basal area at ground level and M_t is the needle mass of shoots from the upper third of the tree crown at time t.

5. RESULTS

5.1. Descriptive characteristics of advance regeneration

A review of selected literature was done on the relationships between different tree variables and ecophysiological factors that affect the response and acclimation of the advance regeneration of Norway spruce to release (**I**).

The morphometric attributes of needles and shoots of the same year and same tree were correlated (**II**). The various shoot characteristics are strongly correlated and highly dependent on growing conditions, particularly light, and a correlation subsists between shoot length and needle mass and other shoot variables of the current and consecutive years. The length of the shoot and number of needles on the shoot ($r = 0.93$) and the length and the needle mass of the shoot ($r = 0.91$) were the most strongly correlated shoot variables (**III**).

Specific needle area, i.e., needle area per unit biomass, and the ratio between needle thickness and width, can be used as indicators of needle structure. This can also be used to identify the acclimation of trees to variations in light conditions. Needles were thin and wide in heavy shading, width being nearly three times greater than thickness when the light intensity was 25% of that in the open area. In the open area, the ratio between needle tickness and width was almost 1 (Greis and Kellomäki, 1981).

Needle length was not sensitive to the light environment, whereas needle width increased with light availability (Stenberg et al., 1998; Niinemets and Kull, 1995a). Stenberg et al. (1998) found that needle width and thickness increased with canopy openness. However, the relation between needle thickness and light was not significant. In Norway spruce, needle width was more responsive to irradiance than needle thickness, which was found to be lower in shade needles than in sun needles, while the ratio of needle thickness to width was greater for sun needles (Niinemets and Kull, 1995a; Niinemets, 1997).

The basic shoot characteristics were provided (Figures 1-3). Plot 4 data were not analysed for the papers. The continued measurements enabled calculation of the values for 2004-2007. The variation in tree dimensions was quite high. Plot 2 variables had higher values because the measurements on this plot started in the second year at full light. The mean values of the shoot characteristics generally show an increasing trend, except plot 3 beneath a dense canopy cover. The dry year of 1999 (Period 4) stands out as an exception on plot 1.

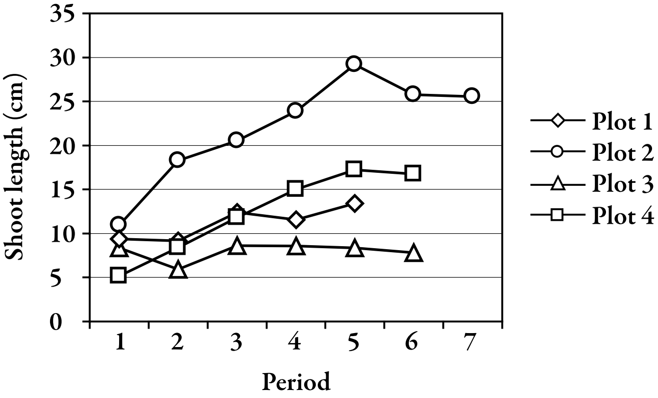

Figure 1. Mean shoot length by period on permanent sample plots.

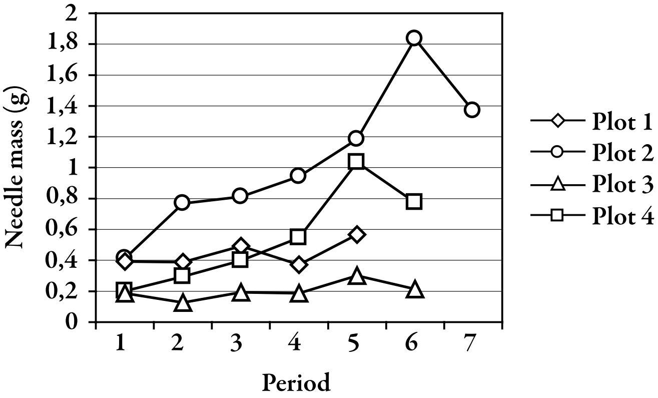

Figure 2. Mean needle mass of the shoot by period on permanent sample plots.

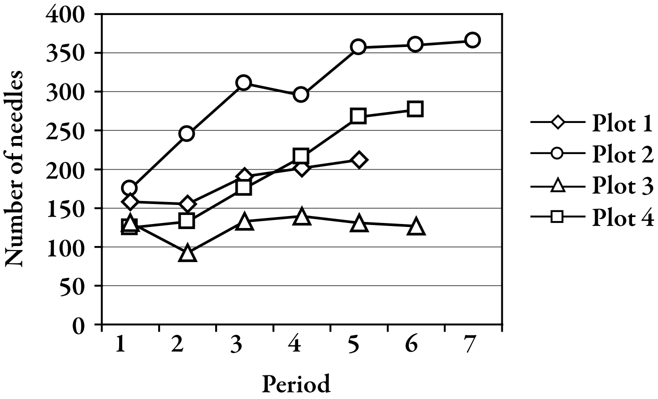

Figure 3. Number of needles of the shoot by period on permanent sample plots.

The basic characteristics of the sample advance regeneration trees are shown in Figures 4 and 5. The values were also calculated for 2004-2007. The variations in tree dimension were quite high.

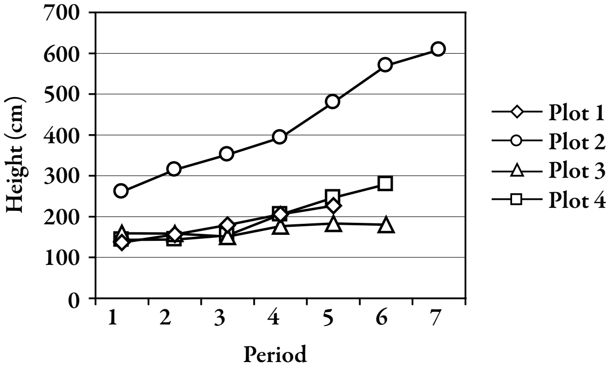

Figure 4. Mean height of the trees by period on permanent sample plots.

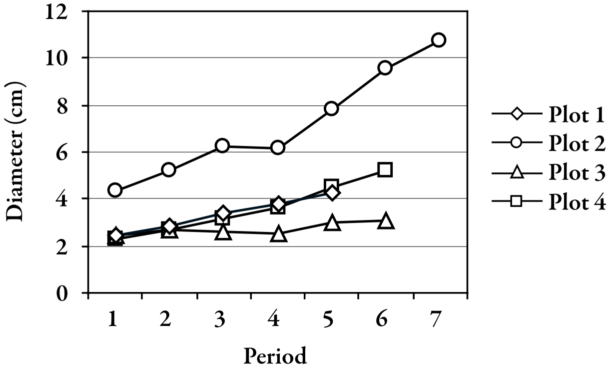

Figure 5. Mean diameter of the trees by period on permanent sample plots.

Table 2 shows the average values and variations in needle characteristics. The standard deviation shows very high variation, because of contrasting properties of trees from shade and light.

Table 2. Summary characteristics of Norway spruce acclimation indicators (**III**).

	Average	Minimum	Maximum	Standard Deviation
L (cm)	12.18	1.50	37.8	7.17
M (cm)	0.48	0.02	1.83	0.36
N	190.01	33	527	98.90
N/L	16.4	3.95	45.08	3.49
M/N	0.22	0.03	0.61	0.09

Note: *L* =length of the shoot; *M* =needle mass of the shoot; *N* =number of needles on the shoot; *N/L* =number of needles per 1 cm of shoot length; *M/N* =hundred needle mass.

Table 3 shows that the correlation between the current-year (same year) needle and shoot characteristics was high. The highest correlations were found between the length of the shoot and number of needles on the shoot (r = 0.93) and length of the shoot and needle mass of the shoot (r = 0.91). The correlation between the diameter increment of the tree and the various shoot variables of the same year was somewhat lower.

Table 3. Correlation matrix of shoot variables of the same year (**III**).

	I_t (mm year^{-1})	L_t (cm)	M_t (g)	N_t
I_t (mm year^{-1})	1			
L_t (cm)	0.652	1		
M_t (g)	0.651	0.908	1	
N_t	0.634	0.926	0.871	1

Note: I_t =diameter increment; L_t =length of the shoot; M_t =needle mass of the shoot; N_t =number of needles on the shoot.

The correlations of shoot variables of the consecutive years are given in Table 4. The correlation between observed characteristics is high. That between different years of same variables had the highest correlation index (r), although the length of the shoot of previous year was strongly correlated with the number of needles on next year's shoot . The tree diameter seems to explain the following year's shoot characteristics better than the reverse.

Table 4. Correlation matrix of shoot variables of the consecutive years (**III**).

	I_{t+1} (mm year^{-1})	L_{t+1} (cm)	M_{t+1} (g)	N_{t+1}
I_t (mm year^{-1})	0.733	0.669	0.661	0.669
L_t (cm)	0.608	0.772	0.714	0.762
M_t (g)	0.638	0.720	0.730	0.716
N_t	0.587	0.721	0.680	0.755

Note: I_{t+1} =diameter increment of next year; L_{t+1} =length of next year's shoot; M_{t+1} =needle mass of next year's shoot; N_{t+1} =number of needles of next year's shoot. I_t =diameter increment of previous year; L_t =length of previous year's shoot; M_t =needle mass of previous year's shoot; N_t =number of needles of previous year's shoot.

5.2. Morphological characteristics to describe acclimation

To determine the change in acclimation, the needle mass data was analysed according to time spent in full light conditions (after clear-cutting). Plot data were combined (Table 1) to obtain the regression parameters of relationships between consecutive years. Data was available from two plots for the third and fourth years. The first, second and fifth years were covered by data from a single plot.

The results suggest that growth accelerates after the stand opening, since the shoots are systematically bigger in the latter of the two consecutive years (Figure 6). Data from the fourth year, however, suggested a growth decline, which can be explained by a severe drought in 1999 (Figure 6, year 4). It also seems that shoot growth has fully recovered by the third year, since during the next normal growing season (the fifth year) growth is similar in same-size shoots. However, it is difficult to tell if these are the maximum values.

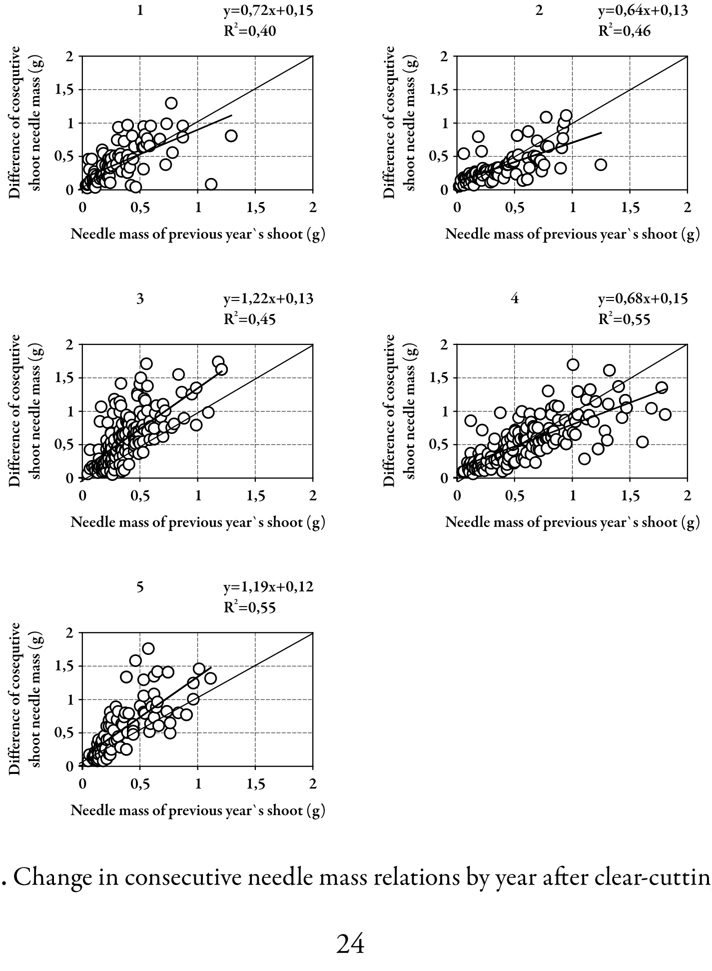

Figure 6. Change in consecutive needle mass relations by year after clear-cutting (**III**).

Figure 7 shows the difference in shoot needle masses of consecutive years. Larger shoots exhibited negative growth, particularly under old canopy and after release. The growth later became stable and the needles could be regarded as becoming acclimated to the new microenvironment. The exception is again the fourth year of growth (Figure 7, year 4), plot 1 data from 1999 reflecting the influence of unfavorable weather conditions. The conditions in year 0 were illustrated by data from plot 3.

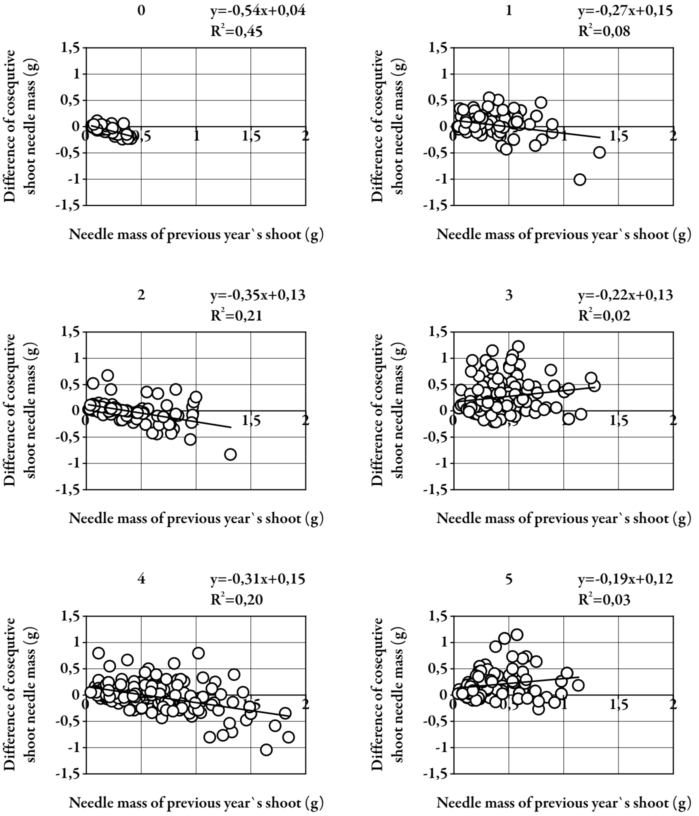

Figure 7. Growth comparison of two consecutive years: difference in shoot needle masses shows the increase, decrease or stability over years (**III**).

5.3. Growth model development

A model was fitted to describe tree shoot development. The best fit for the data was a model with logarithmic transformations of M_{t+1} and M_t (equation 3). Table 5 shows the fitted regression model parameters and the estimated values (n =457, R^2 =0.62, RMSE =0.53).

Table 5. Parameter estimates and associated statistics for the logarithm of needle mass of the shoot model in the next year (t+1) (**III**).

Variable	Coefficient	Value	SE	p-Value
Intercept	a_0	1.480	0.261	<0.005
$\ln M_t$	a_1	0.715	0.056	<0.005
L_t	a_2	0.0002	0.000	<0.005

Note: $\ln M_t$ =logarithm of needle mass of the previous year's shoot; L_t =length of previous year's shoot.

The multiple regression model (equation 4) produced a good prediction for growth (Table 6). The influences of tree, plot and year in the regression models were also considered using dummy variables. Neither the tree and nor the plot influence was significant, and tree, sample plot and year were not significant in the model ($P > 0.05$).

Table 6. Parameter estimates and associated statistics for the logarithm of the basal area increment model in the next year (t+1). Abbreviations: $\ln I_{g(t)}$ is the logarithm of the previous year's basal area increment; K_t is the competition index in the previous year; $\ln G_t$ is the logarithm of the previous year's basal area; and $\ln M$ is logarithm of the previous year's needle mass (**IV**).

Variable	Coefficient	Value	SE	P-value
Intercept	a_0	-0.064	0.340	0.851
$\ln I_{g(t)}$	a_1	0.532	0.044	<0.005
K_t	a_2	-0.014	0.003	<0.005
$\ln G_t$	a_3	0.280	0.055	<0.005
$\ln M_t$	a_4	0.188	0.062	<0.005

The needle mass of the shoots of trees was modelled as follows (n = 453, R^2 = 0.58, RMSE = 0.52):

$$\ln M_{(t+1)} = b_0 + b_1 \ln G_1 + b_2 \ln I_{g(t)} \tag{5}$$

Parameter estimates are given in Table 7.

Table 7. Parameter estimates and associated statistics for the logarithm of needle mass model in the previous year (t-1). ln$G$: is the logarithm of the previous year's basal area; and ln$I_{g(t)}$ is the logarithm of the previous year basal area increment (**IV**; data not shown).

Variable	Coefficient	Value	SE	P-value
Intercept	b_0	3.745	0.144	<0.005
lnG$_t$	b_1	0.111	0.040	<0.005
LnI$_{g(t)}$	b_2	0.296	0.030	<0.005

To model tree height as a function of tree diameter, a regression model of the following type was fitted ($r^2 = 0.89$):

$$H = 56.599D \tag{6}$$

where h is tree height and d is tree diameter at ground level.

Relationships between tree height class and shoot needle mass are shown in Figure 8. Both increment and height class relationships were significant ($R^2 = 0.511$ and $P < 0.0001$; Table 5 in **IV**). The model for the combined effect of both factors showed that R^2 increased to only 0.52. Bigger trees tended to have bigger shoots, but in similar-sized trees (same height class) those with larger diameter growth also had greater needle mass. Both of these variables were highly significant, indicating a correlation between shoot properties and sapling growth.

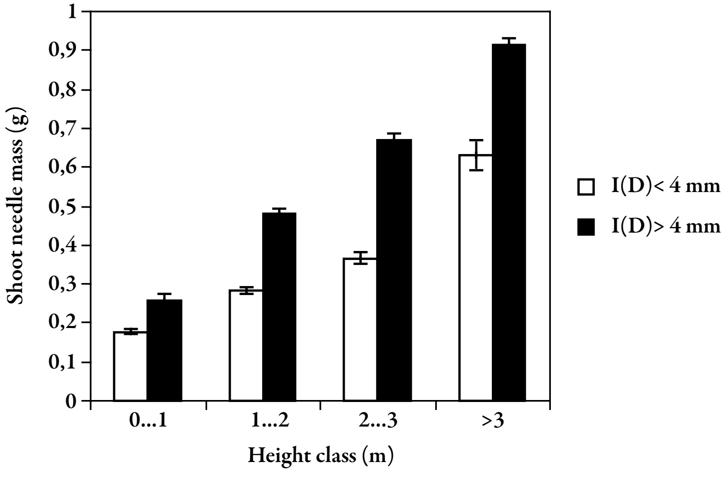

Figure 8. Relationship between tree height class and shoot needle mass. Abbreviation: I(D) = diameter increment (**IV**).

The relationships between basic variables showed considerable correlations (**IV**). There was a tendency observed for higher r^2 values with the period of being in the open.

The competition influence (Figure 9) showed that both tree size and distance from competitor are significant. The influence of competition was greater in the smaller height classes than in the larger. Trees with smaller competition index values had larger diameter increments.

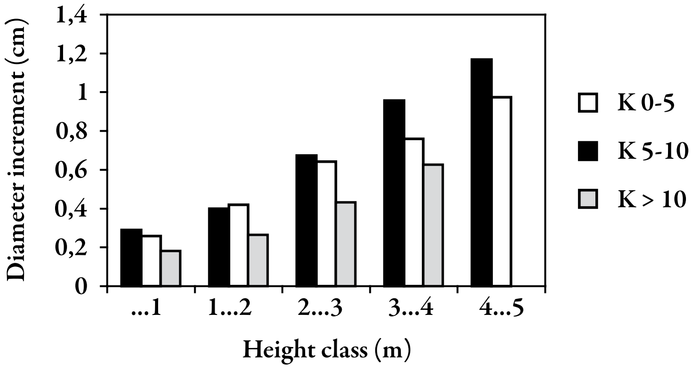

Figure 9. Relationship between height class, diameter increment and competition index (*K*) (**IV**).

To derive the growth trends that follow from the observations, the basal area development of saplings was simulated according to Equation 4. Because the needle mass of the shoot was a variable in the model, the relationships between sapling size, diameter growth and shoot mass were also used to update the shoot characteristics from year to year. Figure 10 shows the simulated growth of trees with three sets of input values, which are described in Table 8. The competition index was constant for all trees during the simulation period. Tree size influenced growth rate to a considerable degree.

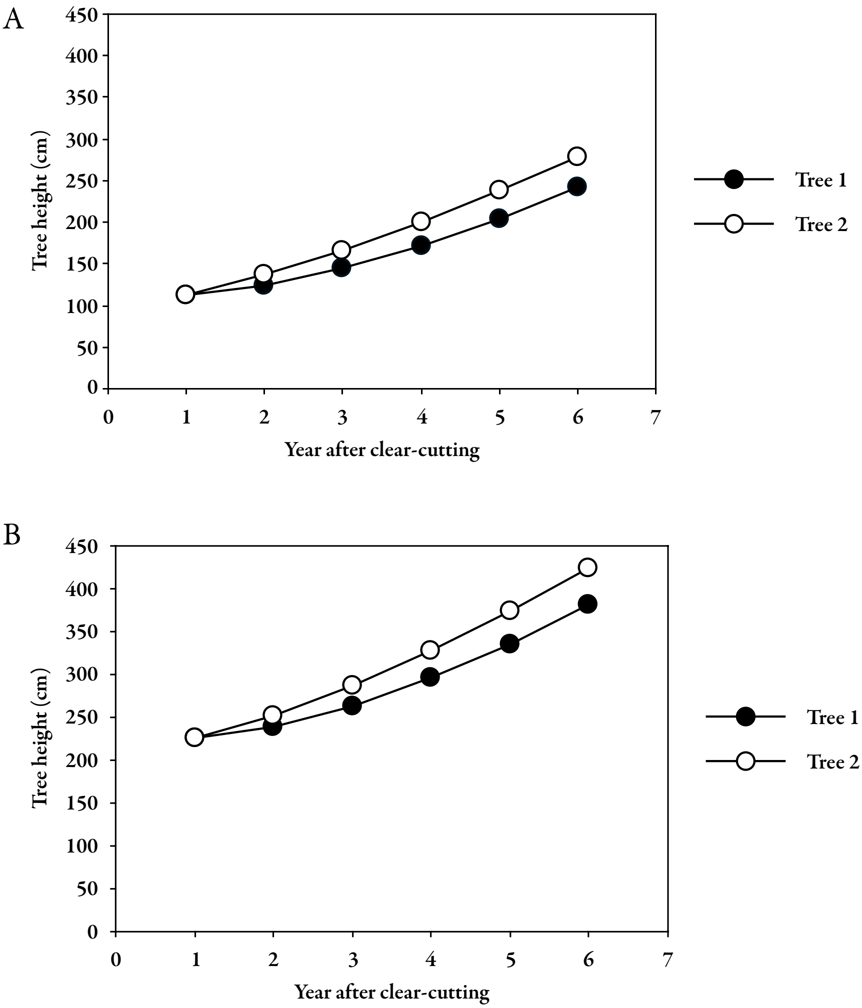

Figure 10. Simulated acceleration in height increment of Norway spruce advance regeneration in the absence of competition according to model (Equation 4) (**IV**).

Table 8. Initial values for the model simulation in Equation 4 (**IV**).

	Basal area (mm^2)	**Diameter (mm)**	**Basal area increment (mm^2)**	**Diameter increment (mm)**	**Needle mass (mg)**	**Competition index**
A						
Tree 1	314	20	32	0.5	600	0
Tree 2	314	20	66	2	600	0
B						
Tree 1	1256	40	64	0.5	600	0
Tree 2	1256	40	129	2	600	0

6. DISCUSSION

Since Norway spruce is able to respond to its current environment by modifying needle structure and function to maximize exploitation of light resources, high phenotypic plasticity is one of its most important characteristics. This growth pattern enables this species to survive in a variety of sites, but at the expense of a reduced growth rate even in the presence of a rich supply of resources (Greis and Kellomäki, 1981). One explanation could be that understorey saplings sacrifice both height and diameter growth in order to allocate a higher percentage of current-year production to needles and shoots (O'Connell and Kelty, 1994).

Shoot growth and the number of needles per shoot are influenced by temperature conditions during the previous summer when the buds were formed; temperature during the current summer affects the length of the needles (Salemaa and Jukola-Sulonen, 1990). Thus, the number of needles and shoot length are very much determined by the mother shoot and its growing conditions during the current year. In the succeeding year, the cells mainly expand (Mauseth, 2003). The growing period of needles is longer and temporarily trails behind shoot extension (Leikola, 1969). For these reasons the current weather conditions appear to have a greater influence on needle expansion than on shoot length growth. However, the shoot extension is very much linked to the temperature regime of the summer, which may cause the separation of factors making the shoot and needle growth difficult (Leikola, 1969; Pietarinen et al., 1982).

The present findings demonstrate that crown, shoot and needle characteristics may reflect acclimation to light conditions and indicate the performance of advance regeneration after release. Light availability, an important factor for seedling establishment, survival and growth, also determining the crown, shoot and needle morphology of Norway spruce trees. The crown morphology of Norway spruce advance regeneration varies from a deep conical crown form in relatively high-light environments to the typical "umbrella" form (short, wide and dense crown) in the understorey shade (under old canopy shade). Shoots and needles developed in shade are flatter and with less self-shading than those developed in light. Needle and branch orientation is horizontal in shade and more vertically inclined in light. The number of nodal and internodal branches increases with increasing light (**I**).

Sun shoots typically have more needle area per unit shoot length than shade shoots and the orientation of needles around the shoot axis is more uniform. Needle inclination is an important stand characteristics as it influences shoot light absorption (Niinemets and Kull, 1995b). In shade shoots, needles are displayed mainly at the sides and the shoot appears to be flat.

The leader-to-lateral shoot ratio reflects changes in tree architecture and is in positive correlation with the amount of light received (Kneeshaw et al., 1998, Parent and Messier, 1995). In high-light environments, trees produce longer leaders relative to lateral branches than trees in low light (Chen et al., 1996). Ratios greater than 1 occur when leaders are longer than average lateral shoots, and an increase in the ratio from one year to the next reflects a change in tree architecture towards a form more adapted to height growth (**I**). However, this ratio is not always the most accurate measure. It is also very important to look at the absolute values.

It is well known that tree shoot characteristics are strongly correlated with and highly dependent on growing conditions, particularly light (Niinemets 1997; Stenberg et al., 1998; 2001; Messier and Nikinmaa, 2000), and this was true in the present study, where the characteristics of sapling shoots grown in similar conditions were very highly correlated. The correlation between shoot needle mass and the previous year's needle volume (same year) suggests the possibility of using single needle growth as an indicator of the acclimation process (**III**). Sellin (2001b) studied sun and shade shoot and needle morphology in more detail.

Immediate but slight acceleration of shoot growth was observed after release; however, the greatest relative change took place between years 2 and 3 (**III**). Selecting shoots from similar topological positions from several saplings and comparing their size between years was used to compare the acclimation of growth between years. In addition, the data from two different experimental set-ups were combined. The populations compared were not exactly the same, which introduces some variation into the results. However, the measurements from the different plots produced similar results. Trees with the smallest shoots appeared to respond most rapidly (**III**). The reason may be that bigger shoots have been growing in sufficient light conditions (light shade) and their size has reached a certain limit and the changes in the structure are relatively slow. Kneeshaw et al. (2002) also found that the growth reduction was dynamically stronger and lasted longer in large than in small seedlings. By the end of the year 5, the whole shoot population seemed to be growing larger than a similar population during the previous year. Valkonen et al. (1998) reported that the time for estimating tree growth should be at least 5 years. Similarly, Tucker et al. (1987) reported that within 2-5 years released Pacific silver fir (*Abies amabilis*) trees showed larger shoot and leader increments than they did before release.

Tree needle mass alone is not sufficient as a predictive variable either for the first or subsequent growth periods, some additional variables on tree size and competition being needed (**II**). The basal area increment was investigated as a growth variable because it is easy to measure accurately. However, because diameter growth and height growth are correlated, it was possible to use the prognostic value of the height increment of the previous year in the model (**IV**). Height increment has also been used as a mortality predictor (Ruel et al., 1995). Comparing the empirical trends with the model runs, it is possible to detect considerable differences (Figure 1 and Figure 10). However, the distribution of the residuals did not reveal any bias in the model predictions (Metslaid 2004).

It was observed that basal area growth was correlated with shoot properties in the upper third of the crown. In similar-sized saplings, basal area growth was more pronounced if the shoots showed vigorous growth, indicating that shoot structure may mean overall acclimation to the changed conditions (**IV**). Shoot growth depends on local light conditions, position within the stem and the overall tree growth (Nikinmaa et al., 2003). Shoots from a similar position in saplings of similar size and growing in similar light conditions are likely to be of similar size. However, following release, the understorey saplings are subjected to a major environmental change that influences shoot structure. For example, while solar irradiance influences needle packing on shoots (Niinemets, 1997), shoot growth depends on tree growth, especially in Norway spruce, which has a plastic crown structure that is dependent on light conditions (Sellin, 2001b). Kneeshaw et al. (2002) observed that understorey release causes an immediate growth response in roots but a more gradual response in aerial tree parts. The degree of shoot vigour could indicate the degree of acclimation of the sapling to the new growing conditions. Kneeshaw et al. (2002) also found that larger individuals experienced a greater growth reduction during the first post-harvest growing period than smaller individuals. In present study, although the basal area increment showed a clear tendency to increase in all trees, the timing of growth resumption depended on previous growth (**IV**).

It was also found that competition slowed sapling recovery (**IV**). Lundqvist and Fridman (1996) concluded that competition probably begins around breast height in uneven-aged Norway spruce stands, which is also the size range of the advance regeneration in this study. Competition eventually leads to self-thinning (Ray et al., 1999). Because understorey saplings often occur in patches that have established themselves in previous canopy openings, the present results suggest that sapling recovery after release could be accelerated by sapling density control in the patches (**IV**).

Correlation between the shoot size and properties means that the reaction of saplings to release can be predicted from tree size and the growing environment (degree of shading) in the understorey and the shoot size and shoot growth after understorey release, along with sapling size and competition from surrounding plants (**IV**). Sapling age also may have a role in acclimation, especially in trees that have very long-lived leaves such as Norway spruce. Niinemets and Kull (1995a) found that the needle structure of younger plants changed more rapidly (1-10 years old) than that of older plants (over 10 years old).

Norway spruce is one of the most common tree species regenerating in canopy gaps. Although the influence of gap size on advance regeneration growth was not explicitly estimated, gap size was present in the analysis because it influenced the initial sapling properties before clear-cutting. Coates (2002) found that tree abundance and species composition appear to be controlled more by differentiation among growth and survival niches than by regeneration niches. Gap size is an important determining factor for tree survival, because growth increment is suppressed in small gaps and only shade-tolerant species can survive until light conditions improve (Messier et al., 1999; Coates, 2000). Small gaps may be easily closed by the crowns of surrounding trees, creating unfavorable growth conditions for those saplings that gained the most height when the gap opened (Lieffers et al., 1996). In the present study, this was manifested as variations in the initial size and growth rate before release and was reflected in sapling performance after the clear-cut (see Figure 10).

Silvicultural practices are directed towards enhancing the growth and survival of the advance regeneration trees to re-establish the stand after release (Page et al., 2001). Seedling dynamics and regeneration success do not simply depend on establishment and mortality; shoot growth is also an important factor because it will determine the competitive status of the saplings (Claveau et al., 2002). As the needle mass characteristics are correlated with growth and reflect productive capacity, they are essential variables describing stand regeneration. The capacity of Norway spruce to react to the greater availability of light influences establishment success in stand formation. Drobyshev (2001) points out the strong competition by hardwoods in canopy gaps in the southern taiga region. Observations in the present study seemed to indicate that crown growth recovers within 5 years of the release even with the largest saplings (those with the largest shoots) on the sample plots (**III**).

When released from overstorey competition by a windstorm or regeneration cut, advance regeneration is able to occupy the available growing space and to form a new stand. Shoot and needle morphology can reflect the relative growth and acclimation to new environmental conditions. As shoot characteristics are able to indicate variation in the shading experienced, models that include indicators of shoot properties, sapling size and competition after release are more powerful in predicting sapling recovery (acclimation) after release than those just using such things as size as a predictor (**I**).

7. CONCLUSIONS

Crown, shoot and needle characteristics (morphology) can reflect relative growth, acclimation to different light conditions and indicate the performance of advance regeneration after release. Needle mass and shoot length in consecutive years help to describe the dynamics of the advance regeneration response (**I, III**).

Factors included in the growth model (diameter increment, diameter, cometition and needle mass) predict accelerating height growth. Also empirical height growth demonstrates acceleration. The rapid acclimation of the new shoots of Norway spruce to release seemed to take place within 4-5 years (clear-cut) (**III**).

As shoot characteristics are able to indicate variation in the shading (light conditions) experienced, models that include indicators of shoot properties, sapling size and competition after release are more powerful in predicting sapling recovery after release than just those using indicators like size as a predictor (**I**).

A better understanding of the response and acclimation of Norway spruce advance regeneration and natural processes within forest stands could improve the ability to manage ecosystems in the future, and improve existing silvicultural systems. Studies that examine the growth response of advance regeneration and processes within stands may form a basis for developing silvicultural systems that emulate the natural dynamics of forest ecosystems (**I**).

The most viable trees in these dense patches can be identified by previous growth (both lateral and leader lengths), tree size, crown properties, shoot and needle characteristics (needle number and mass per unit shoot length) (**I, IV**).

Advance regeneration trees can be used for forest regeneration, but competition control (particularly reducing the proportion of fast-growing hardwoods) is required (**IV**). A practical implication is the need to tend dense groups of advance regeneration and to remove competition by other advance regeneration and deciduous trees (**IV**).

A practical implication would be to apply selection cutting, focusing on single trees or groups of trees, or a shelterwood cutting system. In the areas where different regeneration cutting systems (clearcut, shelterwood cutting, etc.) are used, the advance regeneration can be saved during the logging operations.

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SUMMARY IN ESTONIAN

Looduslähedase metsamajanduse üheks oluliseks aspektiks on loodusliku uuenduse kasutamine metsade uuendamisel. Loodusliku uuenduse olemasolu tagab antud piirkonnale omase elupaigalise ja liigilise mitmekesisuse ning metsade genofondi säilimise. Loodusliku uuenduse säilitamine metsakasvatuslike (metsamajanduslike) tööde käigus on oluline aspekt uuendusraiete planeerimisel. Sellise struktuuriga metsad on ka haigustele vähem vastuvõtlikud ja tormikindlamad.

Metsanduse praktikas on raietööde käigus soovitatav säilitada olemasolevat elujõulist eeluuendust (järelkasvu). Samas tekib küsimus, kuidas harvendada tihedaid eeluuenduse gruppe ja millised on peamised eeluuenduse puude visuaalselt määratavad tunnused, mille põhjal me võiksime otsuseid teha (tuleviku puude valimisel)?

Käesolev uurimistöö on keskendunud metsade loodusliku uuenemise aspektidele ja looduslikku eeluuendust mõjutavate faktorite (tunnuste) analüüsile. Töö peamine eesmärk oli uurida vana metsa varjus kasvava hariliku kuuse eeluuenduse kasvu pärast nende vabastamist lageraie aladel. Töö koosneb kirjanduse ülevaate artiklist (**I**) ja kolmest originaaluuringust (**II-IV**).

Metsa uuendamiseks peale lageraiet (uuendusraiet) on olemas mitmeid võimalusi. Esimene võimalus on raiesmik täielikult kultiveerida, st. istutada puittaimi või külvata seemet kogu raiesmiku pindalale. Teine võimalus on jätta metsastatav ala looduslikule uuenemisele. Kasutada võib ka kahe eelnimetatud meetodi kombinatsiooni.

Puuliigid on erineva varju ja valguse kohastumisega. Võrreldes valgusnõudlike puuliikidega suudavad varjutaluvad puuliigid piiratud valguse tingimustes pikemat aega kasvada ja ellu jääda. Enne vana metsa lageraiet või turberaie viimast järku moodustunud noort metsapõlvkonda nimetatakse eeluuenduseks. Harilik kuusk (*Picea abies* (L.) Karst.) on varjutaluv puuliik, mis suudab anda piisaval hulgal elujõulist eeluuendust. Samas ei ole lihtne leida tunnuseid, mis kirjeldaksid piisava täpsusega eeluuenduse puude arengut lageraie järgselt. Eeluuenduse efektiivseks kasutamiseks on vaja teadmisi faktoritest, mis on olulised uuenduse kasvama minekule ja edasisele arengule. Puistu teket tagava uuenemise korral on nimetatud võte ka majanduslikult õigustatud.

Eeluuenduse edasine areng pärast raiet ja häiringut sõltub mitmetest keskkonnateguritest. Seemnete idanemiseks sobivaid substraadi näitajaid on uurinud paljud autorid. Samuti mõjutab uuenemist (eeluuenduse tekkimist) valgussituatsioon ja häilu olemasolu. Mullapinna niiskustingimusele on tähelepanu juhtinud mitmed autorid. Konkurentsi mõju on vaadeldud mitmetes uurimustes.

Puu võra, võrse ja okka tunnused (morfoloogia) võivad peegeldada eeluuenudse puude suhtelist kasvu, kohanemist erinevate valgustingimustega ja nende arengut vabastamisjärgselt. Järjestikuste aastate okkamass ja võrse pikkus kirjeldavad eeluuenduse kasvureaktisooni dünaamikat (**I, III**).

Hariliku kuuse eeluuenduse uute võrsete vabastusjärgne kohanemine toimus 4-5 aasta jooksul pärast lageraiet (**III**).

Kuna võrse tunnused on võimelised peegeldama valgustingimuste varieerumist varjus, mida eeluuenduse puud kogevad, on mudelitel mis prognoosivad puude kohanemist vabastamisjärgselt erinevate võrse tunnuste (näitajate), puu suuruse ja konkurentsi põhjal palju suurem täpsus (prognoosivõime) kui neil mis ennustavad ainult puu suuruse põhjal (**I**).

Kõige parema kasvureaktsiooniga puid on võimalik ära tunda eelmise aasta kasvu (külgvõrse ja ladvavõrse pikkus) puu suuruse ning võrse ja okaste tunnuste (okaste arv ja mass võrse pikkusühiku kohta) järgi (**I, IV**).

Loodusliku eeluuenduse puid on võimalik kasutada metsa uuendamisel, kuid vajalik on konkurentsi reguleerimine, eriti kiirekasvulise lehtpuu hulga vähendamine (**IV**). Praktiline soovitus oleks valgustusraie käigus harvendada tihedaid eeluuenduse gruppe ja vähendada teiste eeluuenduse kuuskede ja lehtpuude poolt avaldatavat konkurentsi (**IV**).

Praktilise soovitusena võiks kasutada valikraiet, keskendudes üksikpuudele ja puude gruppidele või turberaiet (nt. aegjärkne raie). Aladel, kus kasutatakse erinevaid uuendusraieviise (lageraie, turberaie), tuleb raietööde käigus säilitada elujõulisi ja hästi kasvavaid hariliku kuuse eeluuenduse puid.

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I

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Tree variables related to growth response and acclimation of advance regeneration of Norway spruce and other coniferous species after release

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Abstract

Modern forestry has been evolving towards multiple-use of forests and maintenance of biodiversity. Interest in integrating natural forest dynamics into management planning and silvicultural practices has increased as a result of concerns related to biodiversity values and maintaining ecological functions in managed forests. Taking advantage of naturally formed advance regeneration to create a new forest is one way of emulating natural forest dynamics, especially in spruce forests. However, efficient use of advance regeneration requires knowledge about factors influencing their performance. Light is important for growth and for crown, shoot and needle morphology of Norway spruce (*Picea abies*). Crown morphology varies from a conical and deep crown form in relatively high-light environments to the typical ''umbrella'' form in the understorey shade. Shoots and needles developed in shade are flatter and experience less self-shading than those developed in more light. Needle orientation is horizontal in shade and more vertically inclined in light. The number of nodal and internodal branches increases with increasing light. Tree shoot characteristics are strongly correlated and highly dependent on growing conditions, particularly light. There is a correlation between shoot and needle mass and other shoot variables of current and consecutive year's growth. The strongest correlations are between length of the shoot and needle mass of the shoot, and the length of the shoot and number of needles on the shoot. Needle length was not as sensitive to the light environment. However, needle width and thickness increased with canopy openness. This paper presents a review of selected literature on the relationships between different tree variables and ecophysiological factors that influence the response and acclimation of Norway spruce advance regeneration to release. The results indicate that crown, shoot and needle characteristics could reflect the acclimation to light conditions and indicate the performance of advance regeneration after release.

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Keywords: Acclimation; Advance regeneration; Conifers; Morphological characteristics; Norway spruce; Release

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1. Introduction

Natural regeneration is attracting more interest as biodiversity, wildlife habitat preservation, and recreation are increasingly important goals of ecosystem management. Promoting the establishment and growth of advance regeneration offers several advantages. Advance regeneration that responds to release with increased height and diameter growth provides immediate stocking, shade for subsequent seedlings, an aesthetically pleasing landscape, protective cover for wildlife, and soil protection (Ruel et al., 2000). Furthermore, the use of advance regeneration reduces rotation length and silvicultural costs (Ferguson and Adams, 1980; Lähde et al., 1999; Jeansson et al., 1989).

Silviculture based on the dynamics and structure of natural forests is called nature-oriented, ecologically oriented, or close-to-nature. Single-tree or group-selection harvests emulates the small-size gap disturbance that has been suggested as an important regeneration mechanism, for example in natural Norway spruce forests of Northern Europe (Kuuluvainen, 2002). Selection cutting focuses on individual trees or groups of trees, and seed-tree or shelterwood cutting systems operate at the stand level in diversity-oriented silviculture (Lähde, 1992; Lähde et al., 1999). The selection system aims at stand structures that consist of seedlings and trees of all ages. The intent is to cut both large and small trees (Jeansson et al., 1989). Trees removed in single-tree selection are replaced by natural advance regeneration (Lundqvist and Fridman, 1996; Dobrowolska, 1998). The use of advance regeneration is not limited to

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selection cutting systems; where even-aged systems, such as clearcutting or shelterwood cutting, are used, advance regeneration can be relied on if care is taken to protect the saplings during the logging operation.

The use of advance regeneration in silviculture requires that enough saplings establish under the canopy, and that they are able to respond favourably to subsequent canopy openings created by disturbance (an abrupt change in the forest biota and environment, *sensu* Frelich, 2002). The success of advance regeneration varies with the type of disturbance. In boreal forests, various types of small-scale and large-scale disturbances occur, which create openings in forest stands. Disturbances are important in the development of a new stand, since they create growing space by eliminating plants that previously occupied it. Disturbance events such as windstorms, avalanches, or logging operations, which do not completely destroy the forest floor, allow advance regeneration to gain a competitive advantage. When released from overstorey competition by a windstorm, advance regeneration spreads into the newly available growing space and can form a new stand. However, tree responses vary with the interaction between the species and the disturbance (Oliver and Larson, 1996). Both shade-tolerant and shade-intolerant tree species can be found in openings created by a disturbance event (Kneeshaw and Bergeron, 1996), and the composition of the resulting stand depends on how quickly the shade intolerant species can re-establish on the available growing space versus how quickly the advance regeneration can resume growth after release.

Acclimation and further development of advance regeneration after disturbance depend on the properties of the forest environment prior to disturbance and the type of disturbance (e.g., fire) (Tesch and Korpela, 1993; Man'ko, 1967, 2005). Therefore, several models that include different site factors have been developed to model the growth of advance regeneration of Norway spruce (Nyström and Kexi, 1997; Valkonen, 1997). Numerous studies in boreal forests have focused on soil conditions (Brang, 1998; Kneeshaw et al., 2002) and seedbed characteristics (Kneeshaw and Bergeron, 1996; Lieffers et al., 1996; Rooney and Waller, 1998; Cornett et al., 2001; Hanssen, 2003; Brang, 1998; Kneeshaw et al., 2002). Survival of the established saplings, however, depends on the available light and current growth rate (Claveau et al., 2002; Kobe and Coates, 1997). The role of competition has been explored in several studies (Kneeshaw and Bergeron, 1996; Hanssen, 2003; Nilson and Lundqvist, 2001; Duchesneau et al., 2001; Tesch et al., 1993; Grassi and Giannini, 2005).

The species-specific ecophysiological characteristics and their growth pattern determine the response of individuals of advance regeneration to disturbance events. In addition, the acclimation response of advance regeneration reflects growth performance prior to the release. Species that can establish as canopy trees from advance regeneration must have characteristics that enable them to survive in the deep shade of the overstorey and to respond favourably to the increasing light after the overstorey is disturbed. Shade-tolerant tree species normally have low leaf-mass-specific maximum photosynthetic rate and a respiration rate that goes with low mass-specific leaf nitrogen content, high leaf longevity, and low relative growth rate when small, they also are capable of slow growth in adverse conditions with limited root growth (Reich et al., 1992, 1998a; Walters and Reich, 2000; deLucia et al., 1999). As the light reaching the saplings increases, these traits make them less able to compete in new conditions. However, low leaf-specific-net productivity may be compensated for by high leaf longevity, so that as the tree grows, the productivity of these shade-tolerant species may become more comparable to that of species with more efficient but shorter-lived leaves (Reich et al., 1992), thus allowing faster growth. The acclimation, however, is slow because it involves substantial change in leaf size.

Trees with very different rankings in shade tolerance seem to react similarly to changes in light climate (Reich et al., 1998a,b). Important variation in the physiological parameters of productivity depends on the nutritional status of the leaves. Thus changes in growth allocation in different parts of the tree in combination with altered soil and light conditions strongly influence tree growth response following release (Claveau et al., 2002; Kneeshaw et al., 2002). It can take several years after release for secondary (diameter) growth to occur on a tree (Youngblood, 1991). Kneeshaw et al. (2002) found that height growth does not respond immediately after release, but growth reaction is first seen in roots. They also reported that changes in allocation patterns from aboveground to belowground tissues may vary with climate and degree of overstorey removal. These findings are in agreement with the suggestion that trees try to maintain balance between their crown and root system functions (Nikinmaa, 1992). An increase in the growth of structural roots is also believed to counterbalance sway and prevent blowdown (Coutts, 1987). As relative growth rate and size increases, wood versus leaf allocation starts to become a more important determinant of the sapling performance (Mäkelä, 1988; Nikinmaa et al., 2003).

Numerous variables have been tested to explain the mortality and growth of advance regeneration after release. The most frequently proposed attributes are height, age, live crown ratio, and height or diameter growth before harvest (Ruel et al., 1995). Previous growth and growth tendencies of the tree have been used in empirical individual-tree growth models to predict subsequent growth (Pukkala and Kolström, 1991). However, leaf and needle morphology and crown architecture also can characterize the relative growth and acclimation to new conditions (Parent and Messier, 1995; Reich et al., 1998a). Combining these structural characteristics with plant physiology may allow us to develop predictive tools that would facilitate derivation of practical recommendations for the management of advance regeneration. As forest managers learn more about species' success in regenerating after disturbances, they can emulate disturbance patterns in forest management decisions (Fujimori, 2001; Wei et al., 2003; Jõgiste et al., 2005).

In boreal Europe, Norway spruce is the only species with characteristics that allow the use of advance regeneration in its silviculture. This paper reviews selected literature on the relationships between different tree variables and ecophysiological factors that influence the response of advance regeneration of Norway spruce and other coniferous species to release. The particular questions of interest are how Norway spruce compares to other species in its acclimation to understorey conditions and subsequent release, and how these features could be used to predict the sapling performance after release.

2. Review of literature

2.1. Canopy and sapling light availability

The density of a stand's canopy influences the light conditions (light availability) in the understorey. The amount of light received by understorey is an important factor for seedling establishment, survival and growth. Small saplings of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) had light compensation points as low as at 1–2% of full sunlight, although the bigger saplings had considerably higher light requirement (e.g., Messier and Nikinmaa, 2000). In general, at least 20% of full sunlight is required for trees to reach the dominant crown layer (Barnes et al., 1998). Norway spruce is a shade-tolerant species that can exist as advance regeneration under the dense canopy of a mature forest stand (Jeansson et al., 1989; Valkonen et al., 1998). Norway spruce can establish under light demanding species, e.g., *birch* (Rubtsov et al., 2005). Natural death or a windthrow of single trees or groups of trees in the forest stand creates a canopy opening (canopy gap) that favours the establishment of natural regeneration and the existing advance regeneration (Hytteborn et al., 1987; Leemans, 1991; Coates, 2002). Norway spruce is one of the most common tree species to fill in gaps in forests of Northern Eurasia (Liu and Hytteborn, 1991; Drobyshev, 1999).

2.2. Crown properties

Lesinski and Sundkvist (1992) studied the crown morphology of Norway spruce advance growth and found the most frequent (52%) was symmetrical and conically shaped crown. Two other types were crowns that were divided into a higher and a lower part, separated by a branchless portion of stem, and a symmetrical, short, wide and dense crown (umbrella form). Grassi and Giannini (2005) showed the importance of light on growth and morphology of crowns, shoots and needles of Norway spruce and silver fir (*Abies alba*) saplings. In both species, crown morphology varied from a conical and deep crown form in relatively high-light environments to the typical ''umbrella'' form in the understorey shade. The form of trees in low light environments (understorey) is such that yearly branch increment is greater than height increment; hence crown width is frequently greater than 150% of stem height and three times crown depth (Tucker et al., 1987). Similarly, shoots and needles developed in shade are flatter and with less self-shading than those developed in light (Grassi and Giannini, 2005). Norway spruce crown types are showed in Figs. 1 and 2.

In understorey trees, needle and branch angles are almost completely horizontal and the crown is broad and shallow (O'Connell and Kelty, 1994). Trees have an arrangement of foliage that nearly maximizes total daily photon flux density on the foliage from directly above the sapling. Due to longer light beam path length with lower angles, only a small proportion of light passes through the canopy and therefore the light climate is dominated by light from directly above the saplings

Fig. 1. Heavily shaded Norway spruce with ''umbrella'' crown type.

Fig. 2. Open-grown Norway spruce (developing conical, regular crown).

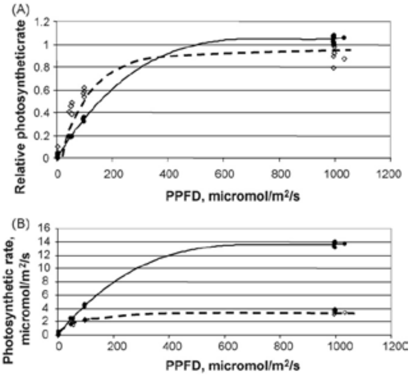

Fig. 3. Norway spruce photosynthetic rate relative to maximum rate (A) and photosynthetic rate (B) at the top of the tree crown (solid line and filled diamonds) and at the lower canopy (dashed line and open diamonds). PPFD is photosynthetic photon flux density.

(Duchesneau et al., 2001; Grassi and Giannini, 2005). On the sun-acclimated trees (open-grown trees) there is substantial self-shading within crown for any given shoot, with the exception of the topmost part of the tree (Tucker et al., 1987). Fig. 3 demonstrates Norway spruce relative photosynthetic rate and photosynthetic efficiency of shoots with different acclimation (different positions in tree crown; original data).

Internodal branches are important to increase the total foliage area in a high-light environment. Duchesneau et al. (2001) found that 25% of full sunlight was required to produce at least one internodal branch in balsam fir (*Abies balsamea*). Also, the number of nodal and internodal branches increases with photosynthetic photon flux density in this species (Parent and Messier, 1995). In contrast to spruce, Scots pine (*Pinus sylvestris*) advance regeneration increases branch growth after release, albeit with delay (Sundkvist, 1994). Similarly, Kneeshaw et al. (1998) found that an increase in the number of branches produced did not occur until 2 years had passed in Jack pine (*Pinus banksiana*) and Douglas-fir (*Pseudotsuga mensizieii*). Long-term response to a prolonged increase in light in spruce would include an overall increase in the number of branches produced, in addition to increases in height growth and the ratio of leader to lateral branches (Kneeshaw et al., 1998).

2.3. Effect of shading on shoot and branch properties

Leader-to-lateral branch ratio reflects changes in tree architecture and is in positive correlation with the amount of light received (Parent and Messier, 1995; Klinka et al., 1992; Kneeshaw et al., 1998). Balsam fir (*A. balsamea*) follows a similar growth pattern as Norway spruce. Understorey trees have a lower degree of apical control (O'Connell and Kelty, 1994). In high-light environments, trees produce longer leaders relative to lateral branches than do trees in low light (Chen et al., 1996). Ratios greater than 1 occur when leaders are longer than the average of lateral branch lengths and any increase in the ratio from 1 year to the next year reflects a change in architecture towards a form more adapted to height growth. Grassi and Giannini (2005) found that the last 3 years' average apical dominance ratio (ADR) is the simplest indicator for Norway spruce of the light conditions in which the tree is growing. A value of ADR = 1, corresponding to a relative irradiance of about 15–20%, may be used as a simple threshold to evaluate whether a sapling is likely to be considered light-stressed. This parameter is easy to measure and in the examined conditions does not change significantly with sapling height or competition (Grassi and Giannini, 2005). The growth differences between leader and lateral branches as a function of received light extends also to branch axes of different order. In heavy shading, the growth rate of the second-order lateral is greater than that of the first-order lateral (Greis and Kellomäki, 1981).

The different shoot characteristics are also strongly correlated and they depend on growing conditions, particularly light (Niinemets and Kull, 1995a; Stenberg et al., 1998; Stenberg et al., 2001; Messier and Nikinmaa, 2000). The length of the shoot and number of needles on the shoot ($r = 0.93$) and length of the shoot and needle mass of the shoot ($r = 0.91$) were the highest correlated shoot variables in trees that had been growing in a variable understorey environment (Metslaid et al., 2005a). Niinemets and Kull (1995b) found that needle number per unit shoot length increases with increasing irradiance and total tree height. The shoot length slightly decreases with increasing tree height, but not significantly, and shoot length did not correlate with the needle number per unit shoot length (Niinemets and Kull, 1995b). The average shoot size in the understorey was smaller in heavier shade (Metslaid et al., 2005b). The average volume of the needles decreased more than the shoot needle mass with increasing shade, indicating that shoot size was less influenced than needle properties. Metslaid et al. (2005a) found that bigger trees tended to have bigger shoots, but the correlation of tree diameter increment with different variables of shoots of the same year was only moderate (Metslaid et al., 2005b). In trees with similar height, those with larger diameter growth also had greater foliage mass.

Sun shoots typically have more needle area per unit shoot length than do shade shoots, and the orientation of needles around the shoot axis is more uniform. Needle inclination is an important stand characteristic as it influences shoot light absorption (Niinemets and Kull, 1995b). In shade shoots, needles are displayed mainly at the sides and the shoot appears to be flat (Stenberg et al., 1999). The vertical inclination of the needles depended on prevailing light conditions. In heavy shade the needle inclination was about 5°, and in the open, 45° (Greis and Kellomäki, 1981).

2.4. Effect of shading on the characteristics of needles

Specific needle area, i.e., needle area per unit biomass, and the ratio between needle thickness and width, can be used as indicators of needle structure. It is also one of the principal mechanisms by which different tree species acclimate to variations in light conditions (Reich et al., 1998a,b). Greis and Kellomäki (1981) found that needles were thin and wide in heavy shading; needle width was nearly three times greater than needle thickness when the light intensity was 25% of that in the open area. In an open, free-to-grow environment, the ratio between needle thickness and width was almost 1, making the shape of the cross-sectional cut of the needles resemble a square.

Duchesneau et al. (2001) showed that light availability does not substantially affect needle surface area of a single needle, confirming earlier reports for a wide range of plant species (Niinemets and Kull, 1994). At the same time, specific leaf area increased in low-light environments (Chen et al., 1996). This kind of morphological acclimation usually results in a variation of leaf thickness or specific density of needles. Thinner needles create a bigger surface area for photosynthesis with the same structural investment by the plant, which is advantageous for trees in scarce light conditions (Chen et al., 1996). At the same time it is advantageous to invest in more photosynthetic capacity and area where relative irradiance is high, which leads to a bigger needle number per unit shoot length (Niinemets and Kull, 1995b).

Needle length is not sensitive to the light environment, whereas needle width increases with light availability (Stenberg et al., 1999; Niinemets and Kull, 1995a). In conifers needle thickness generally increases with increasing irradiance (Niinemets, 1997). Stenberg et al. (1999) found that needle width and thickness increased with canopy openness. However, no significant relation was found between needle thickness and irradiance. In Norway spruce, needle width is more responsive to irradiance than needle thickness. Needle width increased significantly with the relative amount of penetrating diffuse solar radiation. Thus the needle thickness/needle width ratio decreased, but the ratio of total and projected needle surface area increased. Needle thickness was found to be lower in shade needles than in sun needles, and the ratio of needle thickness to width was bigger for sun needles (Niinemets and Kull, 1995a; Niinemets, 1997).

Total and projected needle surface areas and needle lengths were not significantly related to irradiance. Needle dry weight per total surface area and per projected surface area increased with increasing relative amount of penetrating diffuse solar radiation and greater tree height. Needle density increased with total tree height. There was no significant correlation between height of needle location and stand density (Niinemets and Kull, 1995a).

Niinemets and Kull (1995a) found no correlation between tree height and relative amount of penetrating diffuse solar radiation, but they found significant correlation between sapling height and light availability. The needle mass per area increases with increasing irradiance and total tree height (Grassi and Giannini, 2005). Also, needle length tends to increase with total tree height, but not significantly (Niinemets and Kull, 1995a). Niinemets and Kull (1995a) reported that the amount of photosynthesizing tissue per unit leaf (needle) weight decreased with increasing tree age or height. Older Norway spruce trees grown in open areas have lower total needle surface area and weight-based photosynthetic capacities than younger trees (Kull and Koppel, 1987).

2.5. Acclimation to release

Norway spruce is able to respond to its current environment by modifying needle structure and functions to maximize exploitation of light resources. Therefore high phenotypic plasticity is one of the most important characteristics of Norway spruce. This growth pattern enables Norway spruce to survive in a variety of sites, but at the expense of a reduced growth rate even in the presence of a rich supply of resources (Greis and Kellomäki, 1981). One explanation could be that understorey saplings sacrifice height and also diameter growth in order to allocate a higher percentage of current-year production to foliage and shoots (O'Connell and Kelty, 1994).

Shoot growth and the number of needles per shoot are influenced by temperature conditions during the previous summer when the buds were formed; temperature during the current summer affects the length of the needles (Salemaa and Jukola-Sulonen, 1990).

Metslaid et al. (2005b) studied the growth reaction after stand opening. After understorey release, the shoots were systematically bigger in the latter of 2 consecutive years. Larger shoots grew more than small ones, while the relative growth remained constant between shoots but was subject to annual variation (Metslaid et al., 2005b). Shoot growth had fully recovered by the third year. By the end of the fifth year, the whole shoot population seemed to be growing bigger than the similar population during the previous year. It also seemed that by year 4 after the release, there was no further increase in shoot growth. Due to correlation of shoot properties within the same year and between consecutive years the shoot properties have high correlation between consecutive years (Jõgiste and Metslaid, 2002; Metslaid et al., 2005b).

Tucker et al. (1987) found that Pacific silver fir (*Abies amabilis*) branch growth recovered in the second growing season, although height growth recovered only in the third growing season following release. This lag of height growth behind branch extension growth may be due to: (1) the time required for physiological adjustment by the apical bud and the subsequent restoration of apical control; (2) an increase in the quantity (or proportion) of sun foliage; (3) the restoration of other functional balances within the tree. Within 2–5 years, however, released trees showed larger branch and leader increments than they did before release. Our studies indicate that the recovery rate in Norway spruce was very similar to that of Pacific silver fir (Tucker et al., 1987).

Due to correlation between the shoot size and properties, the reaction of saplings to release can be predicted from tree size and the growing environment (degree of shading) in the understorey and the shoot size and shoot growth after understorey release, along with sapling size and competition from surrounding plants (Metslaid et al., 2005a). Sapling age also may have a role in acclimation, especially in trees that have very long-lived leaves such as Norway spruce. Niinemets and Kull (1995a) found that needle structure changed more rapidly in younger plants (1–10 years old) than in older plants (over 10 years old).

3. Conclusions

Disturbance events and clear-cut logging often release advance regeneration of various size and age distributions. When released from overstorey competition by a windstorm or a regeneration cut, advance regeneration occupies the newly available growing space and forms a new stand. Acclimation and further growth of advance regeneration trees after a disturbance event depend upon several environmental factors, and light is one of the most important factors for seedling establishment, survival and growth. Shoot and needle morphology can reflect the relative growth and acclimation to new environmental conditions. Therefore, ecophysiological characteristics can be used to describe the response of advance regeneration trees to release.

Norway spruce exhibits acclimative characteristics similar to many other shade-tolerant tree species. The conical crown shape of open growing conditions is reversed to the umbrella form upon loss of apical dominance with decreasing light. The apex versus branch growth has been suggested as an efficient indicator of the shading experienced by a tree, and the potential to respond to release is similar for Norway spruce (Grassi and Giannini, 2005) and balsam fir (Parent and Messier, 1995). Shoot growth is highly correlated with different shoot characteristics, but they are all sensitive to light conditions. As there is a high correlation between shoot and needle mass and other shoot characteristics of current and consecutive years after release, the structural modifications resulting from shading in the understorey have long-term impact on sapling performance after release. Models that use these characteristics as additional predictors of sapling growth better predicted sapling performance after release than models using just size and competition information (Metslaid et al., 2005a).

The fast acclimation of the newest shoots of Norway spruce to the release seemed to take place within 4–5 years after release (Metslaid et al., 2005b) and similarly for silver fir (Tucker et al., 1987). However, the whole plant response is slower in older saplings as the renewal of the whole tree needle properties is slower in older than younger plants (Niinemets and Kull, 1995a). Tree size and age are correlated in similar light conditions but lose the connection in variable light environments. However, as shoot characteristics are able to indicate variation in the shading that is experienced, models that include indicators of shoot properties, sapling size and competition after release are more powerful in predicting the sapling recovery after release than just those using, for example, size as a predictor. As these variables are included in the analysis it is clear that the bigger the saplings that have been in strong shade, the slower the growth response after release (Metslaid et al., 2005a).

Advance regeneration plays an important role in the regeneration strategies used in forest management. Promoting the establishment and growth of advance regeneration offers several ecological and economic advantages. Crown, shoot and needle characteristics reflect the acclimation of advance regeneration trees to different light conditions, and an examination of them can help to predict the performance of trees after release. A better understanding of the response and acclimation of Norway spruce advance regeneration and natural processes within forest stands could improve the ability to manage ecosystems in the future, and improve existing silvicultural systems. Studies that examine the growth response of advance regeneration and processes within stands can form the basis for developing silvicultural systems that emulate the natural dynamics of forest ecosystems.

Practical methods to address the dynamics of growth response and acclimation of advance regeneration would be a useful tool for forest management. The capacity of Norway spruce to react to the greater availability of light influences establishment success and stand formation. Gap development creates a situation in which advance regeneration trees of different acclimation and development status occur in groups. The most viable trees in these dense patches can be identified based on tree size, crown properties, and shoot and needle characteristics (lateral and leader lengths, needle number and mass per unit shoot length). Dense groups of advance regeneration need to be tended and competition by other advance regeneration and deciduous trees removed. A practical implication would be to apply selection cutting, focusing on single trees or groups of trees, or a shelterwood cutting system. In the areas where different regeneration cutting systems (clear-cut, single-tree selection, etc.) are used, the advance regeneration can be saved during the logging operations.

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II

Jõgiste, K., **Metslaid,** M., 2002.

ACCLIMATION OF SPRUCE ADVANCE REGENERATION TO LIGHT CONDITIONS: ESTIMATION BY NEEDLE CHARACTERISTICS.

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Acclimation of spruce advance regeneration to light conditions: estimation by needle characteristics

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Abstract. The growth of trees of spruce advance regeneration growth was measured in consecutive years on a permanent sample plot. The basic acclimation tendencies of needles are described by a dynamic model. The hypothesis on continuous needle recovery was verified. The attributes correlated to age and growth were searched. The needle mass characteristics can reveal the age and thus tree acclimation. The growth model of spruce advance regeneration can be constructed on the basis of needle mass characteristics, tree size and competition indices.

Key words: Norway spruce, acclimation, advance regeneration.

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Introduction

Application of methods close to natural ones to produce a new forest generation has become an important issue in research work. In this connection it is necessary to assess the response of advance regeneration trees to changing conditions after release from old canopy.

Traditional forestry approaches suggest models for the estimation of advance regeneration growth. Usually those models are based on observations of the regeneration phase (Smith et al., 1997).

Norway spruce (*Picea abies* (L.) Karst.) is a shade tolerant tree species, which can produce a viable population of advance regeneration. However, it is not easy to find characteristics describing reliably the performance of advance regeneration trees forming next generation. Traditional forestry descriptors are often quite subjective and the models are debatable. There are few measurements to follow the advance regeneration trees during several years on permanent plots.

The present work addresses the performance of advance regeneration trees and tries to find variables for modelling the growth response of trees. The hypothesis was set that needle mass characteristics of trees can be related to growth data and a model can be based on this relationship. Analysis of needle data is a basis for model building.

Material and methods

An experiment was established in Järvselja Experimental Forest in 1997. A clearcut area was chosen for monitoring advance regeneration of Norway spruce. The area had been cut clear in winter 1995/1996. So the trees had been growing in open conditions for a year already. The main characteristics for old canopy can be described by stand composition: 70% of spruce, 20% of birch (*Betula pendula* Roth) and 10% of aspen (*Populus tremula* L.). The relative density of the old stand was 70%. The advance regeneration trees were chosen in two groups for permanent sampling and measurement. Trees were numbered (tagged with metal labels).

One group consisted of trees from heavy shade of old canopy. The other group represented trees from an old gap. The variables of advance regeneration recorded were tree height, diameter at root collar, living crown base and crown diameter in two directions. In addition the length of the top shoot was recorded.

All measurements made describe the tree condition at the end of seasonal growth (there were two measurements in 1997, in spring and autumn). At each measurement the lateral shoot was taken randomly from the upper third of the canopy for laboratory measurements of needle mass characteristics. The collected shoots are believed to reflect the growth capacity of a tree during the previous year.

Trees were measured during four years. Thus data on five consecutive years became available. At the start of the experiment (1997) the shoots of two previous years (1995 and 1996) were taken and needle mass was analysed.

The needle mass, length and number of needles were recorded in laboratory for each shoot. Five randomly selected needles were measured for volume determination. The needle length, width and thickness were determined and the volume was found by the formula:

$$NV = NL \times NW \times NT \times K, \qquad (1)$$

where NL is needle length, NW is needle width, NT is needle thickness and K is coefficient. The value of K was 0.8. The mean of five volumes was calculated and taken into database as shoot descriptor.

Multiple regression analysis was used to describe relationships between growth parameters of consecutive years.

Results

The advance regeneration trees were described earlier by Kari & Jõgiste (2001). Some basic parameters are given in Table 1. The morphometric attributes of needles and shoots of the same year and same tree were correlated. The needle and shoot correlations are described by Metslaid (2002).

The next step was to compare needle and shoot characteristics of numbered trees of consecutive years. A correlation exists between needle characteristics of consecutive years. This relationship can be utilised in modelling the growth response and regeneration success after clearcutting. Figure 1 demonstrates the shoot needle mass relationships as a function of new shoot needle mass on previous year shoot needle mass of the same tagged trees. A linear regression model of the following form was

Table 1. Basic characteristics of trees (± standard error)

	D	*H*	*Lv*
1996	2.45±0.19	140.80±6.58	3.28±0.16
1998	3.28±0.16	173.73±9.55	30.60±3.17
1999	3.77±0.20	206.59±10.46	42.25±3.53

D, diameter; *H*, height; *Lv*, top shoot length

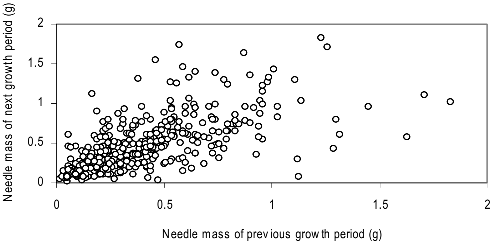

Figure 1. Relationships between needle masses of consecutive years.

fitted to data:

$$M_{t+1} = a_0 + a_1 \times M_t \tag{2}$$

where M_{t+1} is needle mass of new shoot, M_t is needle mass of previous year, a_0 and a_1 are regression coefficients. R^2 of the fitted linear model for predicting needle mass of the new shoot was 0.44. The result (parameter estimations) was highly significant ($p < 0.0005$). Regression statistics are given in Table 2 (Model 1).

Figure 2 shows the shoot length relationships as a function of new shoot length to previous year shoot length of the same tree. The fitted model (analogous with the model in equation 1, with variable *L*, shoot length) demonstrated a higher coefficient of determination: $R^2 = 0.56$ and $p < 0.0005$.

A model of the same type (Model 3, Table 2) was applied to variables NV_{t+1} (needle volume on new shoot) and NV_t (needle volume of previous year). R^2 of this model was the lowest, 0.17, but parameter estimations were highly significant ($p < 0.0005$).

The shoot needle volume was chosen as a function variable and previous needle mass and shoot length together with mean needle volume were used as independent variables. The best model was obtained by the following equation:

$$\ln M_{t+1} = b_0 + b_1 \times \ln M_t + b_2 \times L_t\,, \tag{3}$$

where M_{t+1} is needle mass of new shoot, M_t is needle mass of previous year and L_t is previous shoot length. R^2 was 0.52 and parameter estimations were highly signifi-

Table 2. Regression coefficients of fitted models for consecutive years of shoot and needle estimation

	Intercept		Coefficient		R^2
	Estimated value	*t*-value	Estimated value	*t*-value	
Model 1	0.1495	7.4752	0.7530	18.3272	0.4403
Model 2	2.6453	6.3152	0.8321	23.3900	0.5616
Model 3	2.7837	11.5187	0.4598	9.4117	0.1721

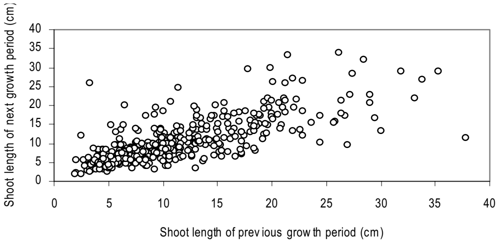

Figure 2. Relationships between shoot lengths of consecutive years.

Table 3. Regression statistics of shoot needle mass change model

Variable	Coefficient	Estimated value	*t*-value
Intercept	b_0	-0.7001	-4.6088
M_t	b_1	0.5545	9.2533
L_t	b_2	0.0271	3.3332

M_t, previous shoot mass; L_t, previous shoot length

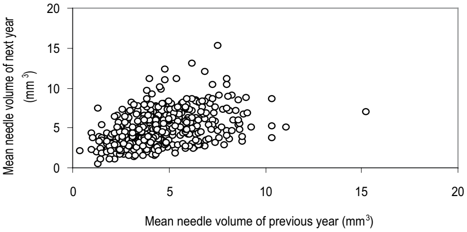

Figure 3. Relationships between needle volume characteristics of consecutive years.

cant ($p < 0.005$). Mean needle volume was removed from analysis as the estimation of the parameter value was not significant. Regression statistics are shown in Table 3.

Needle mass is growing and is correlated with the improvement of radial growth. Needle mass was selected as descriptor of growth capacity. Although other variables can produce higher consecutive correlations the mass is believed to produce biologically reliable prediction.

Discussion

Needle mass characteristics reveal tree acclimation. An acceleration of growth after clearcutting is obvious by the regression characteristics of needle masses. The continuous recovery of needle mass puts also emphasis on modelling perspectives. Decision-making concerning the quality of trees is based on quantitative methods. Although older qualitative models are useful the risk of making wrong decisions and mismanagement is greater.

The further growth acceleration is a function of tree re-acclimation. Re-acclimation depends on the total availability of CO_2 and photosynthetic capacity of a tree.

Needle mass characteristics enable to estimate tree acclimation to shade. The radial or height increment of a tree after clearcutting can be modelled on the basis of needle characteristics.

The time for estimating the tree growth should be at least five years (Valkonen *et al*., 1998). The recovery is a continuous process and a dynamic model can be constructed on the basis of the needle characteristics.

The acclimation to shade conditions cannot be easily determined by earlier increment because the advance regeneration tree age is unknown. Problems faced in the determination of advance growth trees are described by Niklasson (2002).

The regeneration establishment depending on the gap formation is treated by several authors (Coates, 2000, 2002; Lundqvist & Fridman, 1996). Coates (2000, 2002) found that regeneration establishment depends on the gap formation. Lundqvist & Fridman (1996) did not detect any such dependence.

Needle mass alone is not sufficient as predicting variable for the first and also subsequent growth periods. Some additional variables on tree size and competition are needed. The finding that mean needle volume does not contribute to prediction power of a model is surprising and further investigation is needed.

Stand level variables can be obtained on the basis of individual tree measurements. However, a physiological mechanism must be used to interpret the data in the present work. Process based models can provide a basis for the explanation of the present results (Hari *et al*., 1985).

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Kuuse eeluuenduse kohanemine valgustingimustega okkamassi näitajate põhjal

Kalev Jõgiste, Marek Metslaid

Kokkuvõte

Käesolevas artiklis on analüüsitud nelja aasta vaatlusandmeid, mis koguti kuuse eeluuenduse kohanemise määramiseks.

Selgus, et valitud puudelt kogutud võrsete tunnused (iseloomustavad eelmist kasvuperioodi) on suuresti korreleeruvad. Puude kohta mõõdeti järgmised tunnused: puude kõrgus, diameeter juurekaelalt, võra alguse kõrgus, võra läbimõõt kahes suunas. Võrsetel mõõdeti nende pikkus, määrati okaste mass ja loendati okaste arv, samuti mõõdeti viiel juhuslikult valitud okkal paksus, pikkus ja laius okka mahu määramiseks. Analüüsi tulemusena jõuti järeldusele, et järgmise aasta võrse näitajaid (sellest tulenevalt ka kasvukiirust) on võimalik ennustada eelmise aasta andmete põhjal. Koostatud on prognoosiv mudel, mille abil on võimalik ennustada järgneva aasta võrse okaste massi. Mudeli argumentidena kasutati eelmise aasta võrse okaste massi ja võrse pikkust. Funktsiooniargumentidena prooviti ka keskmise okka näitajaid, kuid mudel sellest oluliselt ei paranenud. Mudeli parameetrite hinnangud on statistiliselt olulised ja mudel kirjeldab 52% järgneva aasta juurdekasvu varieeruvusest.

Keskmise okkamahu madal korrelatsioon aastate lõikes on mõnevõrra üllatav ja on vajab edaspidiseid uuringuid.

III

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RECOVERY OF ADVANCE REGENERATION AFTER DISTURBANCES: ACCLIMATION OF NEEDLE CHARACTERISTICS IN PICEA ABIES.

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ORIGINAL ARTICLE

Recovery of advance regeneration after disturbances: Acclimation of needle characteristics in *Picea abies*

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Abstract

This study examined the effect of release on needle properties of Norway spruce advance regeneration in a gap clearing. Needle mass is a variable revealing the acclimation capacity of understorey saplings. Correlations between several needle variables were also examined. A model of needle mass increase over time was developed. Needle mass and shoot length in consecutive years help to describe the dynamics of the advance regeneration response. The analysis suggests that needle and shoot properties had reached new stable conditions 5 years after stand clearance.

Keywords: *Acclimation, advance regeneration, correlation, needle characteristics, Picea abies.*

Introduction

Natural and artificial factors can change the forest environment in a very short time. Such abrupt changes are considered disturbances (Frelich, 2002). Responses of components of forest ecosystems depend on the nature and severity of the disturbances. Disturbances can selectively destroy biota and initiate changes in mutualistic and competitive relations among organisms (Barnes et al., 1998).

Regeneration strategies of trees have evolved in tandem with the prevailing natural disturbance pattern. This pattern thus constitutes a model for forest management decisions (Fujimori, 2001; Wei et al., 2003). The reaction of advance regeneration to disturbance events reflects a species' success in regenerating in openings created by treefalls and provides insight into the possibilities of emulating this disturbance pattern in forest management.

Stand-levelling wind storms and clear-cut logging often leave advance regeneration of varying size and age distribution in place (Frelich, 2002; Abaturov & Melanholin, 2004). The growth of saplings can be modelled after artificial regeneration (Braathe, 1988; Nyström & Kexi, 1997; Valkonen, 1997; Sikström, 2004) or for advance regeneration (Coates, 2000; Wright et al., 2000).

The biggest difference between advance regeneration and seedlings introduced to the site via artificial regeneration is their size distribution. The planted seedlings are of similar size and their above-ground portion has become acclimated to open-growth conditions in the nursery. Stress from transplanting and new soil conditions, however, can have a considerable negative effect on growth (e.g. Kauppi, 1984). Although natural advance regeneration does not suffer from planting stress, after forest clearing seedlings and saplings are subjected to very different growth conditions than their original environment. In response, advance regeneration shows considerable reallocation of resources between shoot and roots (Kneeshaw et al., 2002). Sapling size before stand opening impacts the time it takes for the saplings to adjust to the new growth conditions (Kneeshaw et al., 2002; Metslaid et al., 2005). The allocation changes are associated with several physiological and structural adjustments in the saplings (Reukama, 1959; Ricard et al., 2003).

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Tree vitality and mortality rate are also important factors (Skoklefald, 1967; Ruel et al., 1995; Glöde, 2002).

The basic assumptions for this study are the existence of a correlation between different attributes of tree shoots over different years. Shoot development depends on the local environment and the shoot position within the tree, as well as on the overall growth of the tree (Nikinmaa et al., 2003). When growth conditions remain fairly constant, the shoots of the saplings in corresponding positions resemble each other from year to year. Weather introduces changes into shoot structure (Kanninen, 1984) that cause between-year variations in the shoot attributes. In addition, major changes in the growing environment, such as those caused by disturbances for understorey vegetation, will lead to changes in shoot structure. This type of variation is an important acclimation mechanism for trees (Stenberg et al., 2001) and may also influence sapling growth. Light is generally the most important influence over tree growth in most forested biomes (Denslow & Hartshorn, 1994; Pacala et al., 1996; Lieffers et al., 1999) and is definitely the factor most directly manipulated by forest management actions (Coates & Burton, 1999). It follows that a full understanding of the response of understorey regeneration to light is critical to predicting the impacts of overstorey removals (Marks, 1975; Shugart, 1984; Carter & Klinka, 1992). An analysis of the growth recovery of advance regeneration of Norway spruce (*Picea abies* L. Karst.) (Metslaid et al., 2005) indicated that the recovery of needle characteristics also had an impact on sapling growth.

The main aim of this work was to determine whether shoot and foliage properties describe the dynamics of Norway spruce response to a disturbance event (clear-cut) that exposes them to full sunlight. It was assumed that the sapling condition during the previous year and the growing environment for shoots affect the sapling structure of this year. Further, it was hypothesized that the autocorrelation between structure and growth introduces delay in the capacity of saplings to acclimate to the new environmental conditions.

Needle and shoot characteristics from consecutive years were analysed. It was hypothesized that (1) the lateral shoot mass increased over time, (2) the total mass of lateral shoot needles was dependent on the previous shoot needle mass and length, and (3) the slope of the relationship changed until the saplings were fully acclimated, after which the relationship remained relatively constant.

Materials and methods

Shoots in were sampled three permanent sample plots in the Järvselja Experimental Forest of Estonian Agricultural University, located in south-eastern Estonia (58°25′ N, 27°467′ E) in Tartu county near Lake Peipsi. Järvselja is situated in the temperate zone with a moderately cool and moist climate. The average annual temperature is between 4 and 6°C. The annual precipitation is between 500 and 750 mm, of which about 40–80 mm falls as snow. The active period of vegetation growth (daily air temperature above 5°C) mostly lasts between 170 and 180 days per year.

The first plot (1) was established on a 2.5 ha clear-felled area harvested during winter 1995/96. The site type is *Oxalis–Myrtillus* and the site index bonitet 1. Before felling, the stand consisted of 70% Norway spruce, 20% silver birch (*Betula pendula* Roth) and 10% quaking aspen (*Populus tremula* L.). The volume of the stand before clear-cutting was 338 m^3 ha^{-1}. The stand structure was uneven and there were some gaps in the canopy. Advance regeneration was not distributed evenly over the clear-cut area. Trees were sampled in two patches 40 m apart, a dense group under previously heavy shade and a second patch that was in a canopy gap.

The second plot (2) was established on a 1.1 ha clear-felled area harvested during winter 1999/2000. The site type is *Oxalis–Myrtillus* and the site index bonitet 1. The main canopy was dominated by Norway spruce (90%); Scots pine (*Pinus sylvestris* L.) made up the balance. The volume of the stand before clear-cutting was 288 m^3 ha^{-1}. Most of the advance regeneration trees were located in one large group, but 15 trees were distributed separately in a second group.

The third plot (3) is a 0.6 ha stand situated next to the first plot, but beneath a dense canopy cover. The site index is bonitet 1 and the site type *Oxalis–Myrtillus*. The old canopy was comprised of 60% Norway spruce, 30% quaking aspen (*P. tremula* L.) and 10% silver birch (*B. pendula* Roth). The volume of the stand was 329 m^3 ha^{-1}. The advance regeneration trees of various heights were unevenly distributed in large and small clumps.

Plot size and configuration varied; size was adjusted to accommodate 100 trees that included trees of different sizes and competition status. Because the density of trees and tree size varied, plot size and shape were not fixed. Plots were centred on the groups of advance regeneration trees. All trees within the plot perimeter were measured to include competition effects, but if a group exceeded 100 trees, only a subarea was sampled. In such cases, neighbouring trees of the sample trees that fell outside the sample plot were also measured, if they were within a radius of 2 m from the sampled trees. If the group was too small to include 100 trees, additional trees were selected, which explains why there were some separate groups. The trees were tagged with numbered metal labels and stem locations mapped.

Average tree height varied among plots: 227 cm on plot 1, 352 cm on plot 2, and the lowest average height of 158 cm recorded on plot 3. The advance regeneration was measured for tree height, diameter at the root collar, living crown base and crown diameter in two directions (Table I). In addition, the length of the top shoot (leader) was recorded. Trees on plot 1 were sampled destructively after 5 years' growth in full light conditions. Basal discs were removed and annual rings measured using WINDENDRO (Regent Instruments). Repeated measurements were used at the other plots. For plot 1 there were six remeasurements (1996–2000; for 1995 only shoots were sampled). For plot 2 three periods were recorded (2001–2003; the first year was missed). From plot 3 two periods (2002–2003) were used to characterize advance regeneration under the canopy.

Measurements were made at the end of the growing season; at each remeasurement, a lateral shoot was taken at random from the upper third of the tree canopy for laboratory measurements of needle mass characteristics. This shoot from the upper third of the crown was always compared with a similarly selected shoot from the same tree from the previous year. Shoot length was measured and number of needles counted in the laboratory. Needles were dried at 70°C for 72 h and weighed. Five randomly selected needles were measured for volume determination. The needle length, thickness and width were measured and the volume was calculated by the formula:

$$V = l*w*t*k \qquad (1)$$

where l is needle length, w is needle width, t is needle thickness and k is a coefficient. The value of k was 0.8 (Jõgiste & Metslaid, 2002; Metslaid, 2002). The mean of the five volumes was calculated and entered into the database as shoot descriptor. The shoots of different years were compared by subtracting from the current year shoot the needle mass from the previous year. This value can be interpreted as a growth indicator: positive values indicate an increase in average shoot mass over the years.

Table I. Variables and units used in the study.

Variable	Denomination	Unit
Tree height	H	cm
Tree diameter at root collar	D	cm
Living crown base	LCB	cm
Crown diameter	CD	cm
Top shoot length	TL	cm
Shoot length	L	cm
Needle mass of shoot	M	g
No. of needles	N	
Needle volume of the shoot	V	mm^3
Diameter increment (at ground level)	I	mm^2 $year^{-1}$

Analysis of variance was used to determine the relationships between morphometric attributes of the trees. Correlations were analysed using MSExcel and STATGRAPH (Version 5.0; STSC). Correlation analysis was used to describe relationships between needle and shoot variables and the diameter increment. Correlation matrices were constructed to describe relationships between shoot variables of the same year and consecutive years. The general linear model (GLM) procedure of SAS statistical package (Version 8.0; SAS Institute) was applied to study the relationships between variables. Four different regressors (M_t = shoot needle mass, I_t = diameter increment, N_t = number of needles, L_t = shoot length) were tested as predictors of needle mass growth of the next year (M_{t+1}).

The following regression model was fitted to predict the needle mass of the next year:

$$\ln(M_{t+1}) = a_0 + a_1*\ln(M_t) + a_2*L_t \qquad (2)$$

where M is needle mass of a shoot from the upper third of tree crown (g), L is length of the shoot (cm), and t is the period (years).

Results

The basic characteristics of the trees are provided in Table II. The variation in tree dimensions is quite high. Table III shows the average values and variations in needle characteristics. The standard deviation shows very high variation. Figure 1 shows the relationship between average needle volumes, shoot needle mass and number of stumps in a 2 m radius around the sapling on plot 1. The shoot size was smaller in heavier shade, as evidenced by the higher number of stumps around the shaded sapling. The average volume of needles decreased more than the shoot needle mass with the stump number, indicating that the shoot size was less influenced than the needle properties.

Mean needle mass of the shoots over the years illustrates a generally increasing trend (plot 1, in Figure 2). The dry year of 1999 stands out as an exception, with growth in that year only 80% of the previous year's growth. Weather data are given in Table IV.

Table V shows that the correlation between the current-year needle and shoot characteristics was

Table II. Sample shoot characteristics of Norway spruce advance growth trees.

		Needle mass (g)			Shoot length (cm)			No. of needles		
		Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Plot 1	1996	0.40	0.02	1.29	9.4	2.0	20.7	158.2	40	338
	1997	0.39	0.05	1.26	9.2	1.9	29.0	155.3	41	397
	1998	0.49	0.05	1.83	12.4	2.5	33.8	190.5	38	473
	1999	0.37	0.06	1.11	11.6	3.4	29.0	201.6	76	372
	2000	0.57	0.07	1.73	13.4	2.0	37.8	212.1	39	467
Plot 2	2001	0.41	0.14	1.03	10.9	3.5	18.3	174.5	68	268
	2002	0.77	0.08	1.80	18.3	1.5	33.4	244.6	70	445
	2003	0.81	0.10	1.81	20.5	2.7	36.5	310.3	40	527
Plot 3	2002	0.19	0.05	0.41	8.4	3.7	14.2	131.5	54	230
	2003	0.13	0.03	0.40	5.9	2.6	13.2	92.5	33	178

Table III. Summary characteristics of Norway spruce acclimation indicators.

	Average	Min.	Max.	SD
L	12.18	1.50	37.8	7.17
M	0.48	0.02	1.83	0.36
N	190.01	33	527	98.90
N/*L*	16.4	3.95	45.08	3.49
M/*N*	0.22	0.03	0.61	0.09

Note: L = length of the shoot; M = needle mass of the shoot; N = number of needles of the shoot; N/L = number of needles per 1 cm of shoot length; M/N = hundred needle mass.

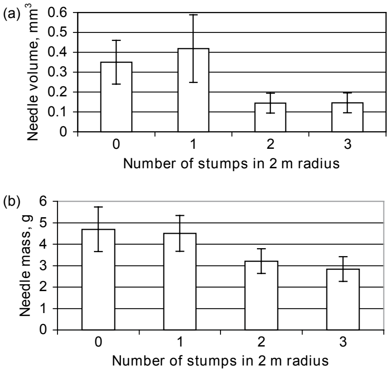

Figure 1. Relationship between needle volume, needle mass and number of stumps.

high. The highest correlations were found between length of the shoot and number of needles of the shoot ($r = 0.93$) and length of the shoot and needle mass of the shoot ($r = 0.91$). Correlation of diameter increment of the tree with different shoot variables of the same year was lower.

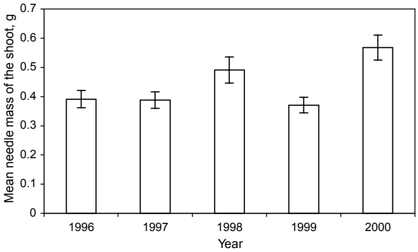

Figure 2. Mean needle mass of the shoot by years on plot 1.

Correlations of different shoot variables of consecutive years are given in Table VI. The correlation is high between observed characteristics. The correlation between different years of same variables had the highest correlation index (r), although the number of needles of the shoot was highly correlated with the length of the shoot. The tree diameter seems to explain better the following year's shoot characteristics than the reverse.

Correlations between needle volume of the same and consecutive years, and the different shoot characteristics of the same year, were also examined. The correlation matrix of needle volume on plot 1 (Table VII) indicates that needle volume and needle mass of the previous year shoot are highly correlated. In large shoots, the needles are also bigger.

To study the change in acclimation the needle mass data were analysed according to time spent in full light (after clear-cutting). Plot data were combined to obtain the regression parameters of relationships between consecutive years. In the third and fourth years data were available from two plots. The first, second and fifth years were covered by data from a single plot. Table VIII explains how annual data were combined.

Table IV. Weather data during the observation period.

Year	Mean temperature (°C)	Total precipitation (mm)
1996	4.4	592.7
1997	5.8	709.7
1998	5.4	834.6
1999	6.7	602.2
2000	7.1	613.6
2001	6.0	823.2
2002	6.3	533.4
2003	5.7	743.6

Table V. Correlation matrix of different shoot variables of the same year.

	I_t	L_t	M_t	N_t
I_t	1			
L_t	0.652	1		
M_t	0.651	0.908	1	
N_t	0.634	0.926	0.871	1

Note: I_t = diameter increment; L_t = length of the shoot; M_t = needle mass of the shoot; N_t = number of needles of the shoot.

Table VI. Correlation matrix of different shoot variables of the consecutive years.

	I_{t+1}	L_{t+1}	M_{t+1},	N_{t+1}
I_t	0.733	0.669	0.661	0.669
L_t	0.608	0.772	0.714	0.762
M_t	0.638	0.720	0.730	0.716
N_t	0.587	0.721	0.680	0.755

Note: I_{t+1} = diameter increment of next year; L_{t+1} = length of the shoot of next year; M_{t+1} = needle mass of the shoot of next year; N_{t+1} = number of needles of the shoot of next year; I_t = diameter increment of previous year; L_t = length of the shoot of previous year; M_t = needle mass of the shoot of previous year; N_t = number of needles of the shoot of previous year.

Table VII. Correlation between shoot variables based on plot 1.

	V_{t+1}	V_t
V_t	0.415	1
L_t	0.411	0.586
M_t	0.463	0.704
N_t	0.381	0.472

Note: V_{t+1} = needle volume of the shoot of next year; V_t = needle volume of the shoot of previous year; L_t = length of the shoot of previous year; M_t = needle mass of the shoot of previous year; N_t = number of needles of the shoot of previous year.

The results suggest that growth accelerates after the stand opening: the shoots are systematically bigger in the latter year of the two consecutive years (Figure 3). Data from the fourth year, however, suggested a growth decline, which can be explained by a nationwide drought in 1999 (Figure 3, year 4; see also Figure 2). It also seems that shoot growth has fully recovered by the third year, since during the next normal growing season (the fifth year) growth is similar in same-size shoots.

Results of multivariate analysis are shown in Table IX ($R^2 = 0.54$, RMSE = 0.21). All regressors separately were able to predict the needle mass with almost the same precision (see pairwise correlations in Table VI). Shoot length is an easily measurable attribute and has potential for use in a model predicting change in needle mass.

A model was fitted to describe tree shoot development. The best fit for the data was a model with logarithmic transformations of M_{t+1} and M_t (eq. 2). The fitted regression model parameters and the estimated values are presented in Table X ($n = 457$, $R^2 = 0.62$, RMSE = 0.53).

The needle mass of next year was not explained with a simple linear model of the needle mass of the previous year as the independent variable. No other single needle characteristic (needle volume or single needle mass) explained the variation.

Larger shoots demonstrated negative growth, particularly under old canopy and after release (Figure 4). Later, the growth became stable and the needles could be regarded as becoming acclimated to the new microenvironment. The exception is again the fourth year of growth (Figure 4, year 4): plot 1 data from 1999 reflect the influence of unfavourable weather conditions. The conditions in year 0 were illustrated with data from plot 3.

Discussion

It is well known that tree shoot characteristics are strongly correlated with and highly dependent on growing conditions, particularly light (Niinemets, 1997; Stenberg et al., 1998, 2001; Messier & Nikinmaa, 2000), and this was true in the present study, where characteristics of sapling shoots grown in similar conditions were very highly correlated. The correlation between shoot needle mass and needle volume points to the possibility of using single needle growth as an indicator of the acclimation process.

The increase in shoot size over the years can be treated as the summation of individual component growth: shoot length, needle size and needle number are attributes describing the change. Shoot length and number of needles correlated quite well over the years studied, although there was less correlation between needle mass and the other two variables. The shoots of Norway spruce follow a deterministic growth pattern, in which all the leaf primordia for next year's growth are formed during bud develop-

Table VIII. Combination of plot data to demonstrate acclimation processes (years linked are indicated according to acclimation time and plot number).

	Year after clear-cut					
Plot no.	0	1	2	3	4	5
1		1996	1997	1998	1999	2000
2				2002	2003	
3	2003					

Note: year in the table indicates the observation year; the previous year was also covered by the data.

ment in the current year (Kanninen, 1984). Thus, the number of needles and shoot length are very much determined by the mother shoot and its growing conditions during the current year. In the following year the preformed cells mainly expand (Mauseth, 2003). The shoot extension is very much linked with the temperature regimen of the summer (Leikola, 1969; Pietarinen et al., 1982). The growing period of needles is longer and also temporarily trails behind shoot extension (Leikola, 1969). For these reasons the current weather conditions appear to have a greater influence on needle expansion than on shoot length growth. Needle structural properties rapidly respond to changes in microenvironmental conditions. Grassi and Minotta (2000) showed immediate structural changes in developing needles as they were transformed from low to high light. The influence of the growing-year conditions on shoot growth is seen very clearly in the present data in the sharply decreased growth of the dry year 1999.

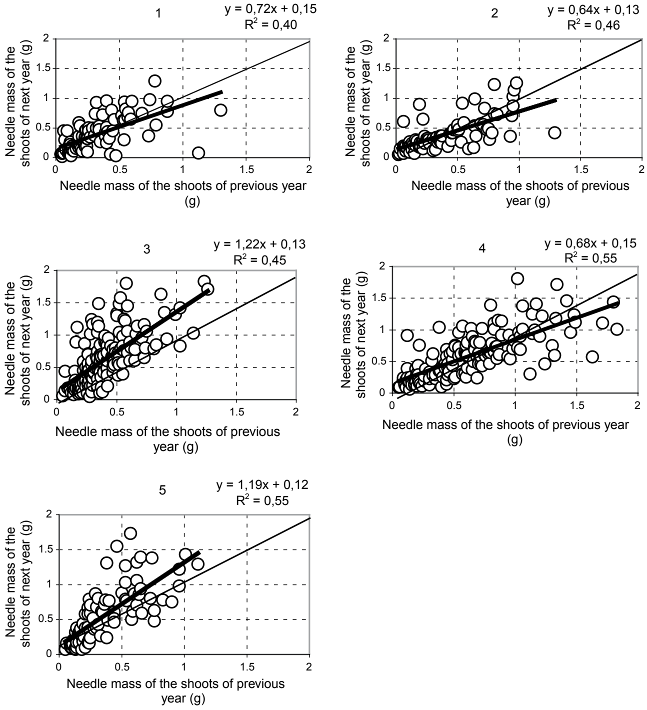

Figure 3. Change in consecutive needle mass relations by years after clear-cutting.

Table IX. Multivariate regression results (type III SS analysis).

Variable	Mean square	F-value	p-Value
I_t	1.63	38.44	<0.0001
L_t	0.09	2.13	0.1450
M_t	0.86	20.21	<0.0001
N_t	1.34	31.50	<0.0001

Note: I_t =diameter increment of previous year; L_t =length of the shoot of previous year; M_t =needle mass of the shoot of previous year; N_t =number of needles of the shoot of previous year. $M(t+1)$ was set as the dependent variable.

Table X. Parameter estimates and associated statistics for the logarithm of needle mass of the shoot model in the next year ($t+1$).

Variable	Coefficient	Value	SE	p-Value
Intercept	a_0	1.480	0.261	<0.005
ln M_t	a_1	0.715	0.056	<0.005
L_t	a_2	0.0002	0.000	<0.005

Note: ln M_t =logarithm of needle mass of the shoot of the previous year; L_t =length of the shoot of the previous year.

Immediate but slight acceleration of shoot growth was observed after release; however, the greatest relative change took place between years 2 and 3. The acclimation of growth between years was compared by selecting shoots from similar topological positions from many saplings and comparing their sizes between years. In addition, the data from two different experimental set-ups were combined. The compared populations are not exactly the same, which introduces some variation into the results. However, the measurements from the different plots produced similar results. Trees with the smallest shoots appeared to respond most rapidly. Kneeshaw et al. (2002) also found that dynamically the growth reduction was stronger and lasted longer in large compared with small seedlings. By the end of the observation period (5 years) the whole shoot population seemed to be growing larger than the similar population during the previous year. It also seemed that by year 4 after the release, there was no further increase in shoot growth (Figure 3).

The slow initial recovery of shoot growth is probably related to overall allocation changes in the tree. Kneeshaw et al. (2002) documented a clear immediate response in the sapling roots after release of the understorey saplings, followed by reaction in the tree crown. Nikinmaa et al. (2003) found that overall shoot growth depends on local light conditions, position within the stem and overall tree growth. Tree ring width explained the following year's shoot characteristics somewhat better than vice versa. This observation could also reflect the importance of below-ground structural limitations in the acclimation to release. As Grassi and Minotta (2000) showed, growing spruce leaves react immediately both physiologically and structurally to increased light conditions, indicating the capacity for increased production. Furthermore, Niinemets (1997) pointed out that growing light conditions determine the shoot structure, while some adjustment in physiology may also take place in older shoots as the environment changes.

In the normal growth pattern of trees, shoot length of the consecutive branching orders tends to decrease (Goulet et al., 1999). As tree size increases, a greater proportion of shoots are those of the higher branching orders. This pattern is important for acclimation of trees with high apical dominance and control such as spruce. Only the development of more horizontal branches will allow efficient capture of irradiation from high elevations. Under a closed canopy, this structure is particularly important as most of the radiation comes from above (Pearcy & Yang, 1996). Upon release, the height growth of saplings becomes more important as slow-growing trees will easily be overtopped by competing vegetation. These changes in crown form are commonly observed in spruce, from umbrella-shaped understorey saplings to sharp conical crowns of typical "Christmas trees". Therefore, the changes in shoot structure observed in this study reflect not only the changes in production potential of the shoots, but also variation in growth pattern from shade to high light. By sampling them from the same topological position every time, the overall decrease in the average shoot size with increasing tree size was avoided. Nonetheless, changes in crown shape probably influenced first the tip growth of lateral branches in the upper crown, which accelerated soon after release, then stabilized.

Silvicultural practices are directed towards enhancing the growth and survival of the advance regeneration to re-establish the stand after release (Page et al., 2001). Seedling dynamics and regeneration success do not depend only on establishment and mortality; shoot growth is also an important factor because it will determine the competitive status of the saplings (Claveau et al., 2002). Because needle mass characteristics are correlated with growth and reflect productive capacity, they are essential variables describing stand regeneration. The capacity of Norway spruce to react to the greater availability of light influences establishment success and stand formation. Drobyshev (2001) points out the strong competition by hardwoods in canopy gaps in the southern taiga region. The present observations seemed to indicate that crown growth is recovered within 5 years of the release even with the largest

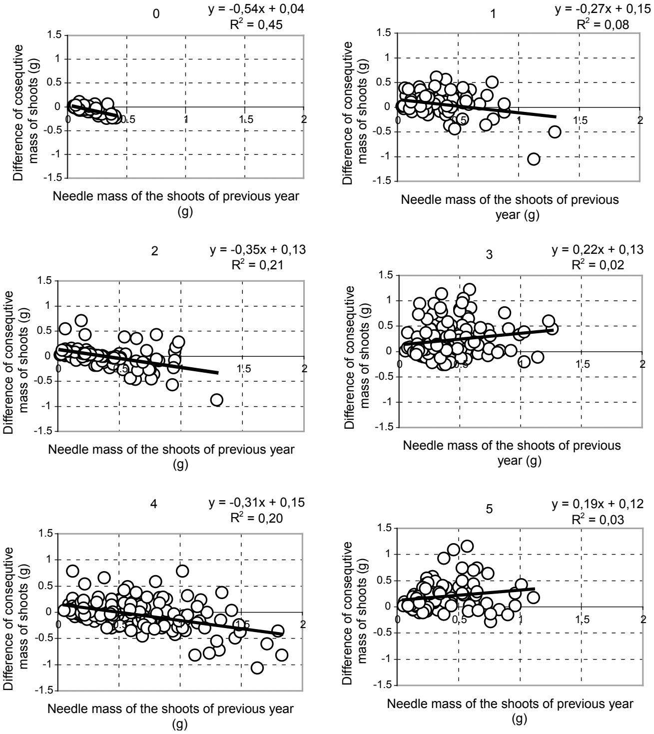

Figure 4. Growth comparison of two consecutive years: difference in shoot needle masses shows the increase, decrease or stability over years.

saplings (those having the largest shoots) in these plots.

Light, however, is not the only factor affecting shoot growth. Sellin (2001) found that understorey spruce saplings were more water limited than saplings growing in open conditions. The impact of overstorey trees on water relations of understorey regeneration has long been considered an important factor (e.g. Frick, 1904; Toumey & Kienholz, 1931; Korstian & Coile, 1938). This limitation may slow down the recovery of dry matter production in the more water-demanding environment of the forest opening until the below-ground water uptake capacity and water transport capacity of the vascular tissue become acclimated to new conditions. Grassi and Minotta (2000) found that nutrient shortage subsequent to the opening of a canopy gap may limit the acclimation response of Norway spruce seedlings. Nitrogen supply is a key factor in the ability of advance regeneration to utilize the improved light conditions associated with overstorey removal. Nitrogen availability may influence the number and length of shoots, the number of needles per shoot, needle lifespan and total foliage mass (Granhus & Brække, 2001). Ingestad and Agren (1991) found that the reduced amount of nitrogen decreased the leaf growth. Granhus and Brække (2001) studied foliar nutrient concentrations of Norway spruce understorey trees after overstorey removal.

Forestry practice in Estonia follows the scale of the life cycle of the main forest trees. It is orientated towards long rotation (cutting age of spruce is 100 years); the gap formation phase (demographic transition *sensu* Frelich, 2002) is included in that cycle. Therefore, advance regeneration plays an important role in the regeneration strategies used in management. Practical methods to address the dynamics of sapling recovery would be a useful tool for forest management. Parent and Messier (1995) suggested that lateral to apical shoot growth could be used for similar purposes. The present results indicate that shoot characterization of the advance regeneration could indicate their recovery capacity and therefore could serve as a potential tool for forest management. In this study needle mass, shoot length and other needle variables were measured, but further work is needed to establish practical recommendations for managers.

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IV

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GROWTH OF ADVANCE REGENERATION OF NORWAY SPRUCE AFTER CLEAR-CUTTING.

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Growth of advance regeneration of Norway spruce after clear-cutting

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Summary We developed a basal area growth model for recovery of advance growth of Norway spruce trees after clear-cutting. Stem diameter growth at ground level and needle-mass characteristics were measured on permanent sample plots in Estonia. Both tree ring analysis (destructive sampling on one sample plot) and yearly repeated measurement data (two plots) were used to quantify advance growth. Basal area growth of small trees was estimated by multiple regression analysis. Previous-year basal area of the tree and basal area growth explained tree performance the next year. Tree needle-mass variables characterizing the acclimation status of the tree were included in the model as explanatory factors. Needle samples (one shoot from the upper third of each tree crown) were collected each year after the growth period from all sample trees. Needle masses of shoots from consecutive years were correlated and this variable was used as a predictor in the simulation model. Accelerating growth was observed in trees that exceeded the growth threshold in the year after release: the greater the needle mass per shoot, the greater the acceleration in growth. Competition among advance regeneration trees was included in the model: small trees under taller neighbors exhibited reduced growth. We found that trees released from a long period of heavy shade can survive, but the time needed for acclimation and resumption of competitive growth rates is considerably longer than for trees released from light shade. Such trees can be used for forest regeneration, but competition control (particularly reducing the proportion of fast-growing hardwoods) is required.

Keywords: acclimation, growth, sapling, shade tolerance.

Introduction

Tree species differ in their patterns of acclimation to shading. Unlike shade-intolerant species, shade-tolerant species can grow and survive for considerable periods in low light (Wright et al. 2000). This advance growth can be utilized for forest regeneration (Greene et al. 2002, Kuuluvainen 2002). Forestry practices in Estonia recommend saving advance regeneration during forestry operations such as logging. However, little is known about how such released trees acclimate to the new environmental conditions or their subsequent growth performance. Furthermore, a scientific basis for developing procedures for tending dense regeneration groups following release is lacking, because the characteristics that could serve as reliable indicators of the performance of advance regeneration after clear-cutting have not been identified and the factors controlling performance of advance regeneration trees after clear-cutting have not been well characterized.

Performance of advance regeneration depends on many environmental factors and several models of advance regeneration growth that include site factors have been developed (Nyström and Kexi 1997, Valkonen 1997). For example, seedbed characteristics (Kneeshaw and Bergeron 1996, Lieffers et al. 1996, Rooney and Waller 1998, Cornett et al. 2001) and soil water conditions have been studied (Brang 1998, Kneeshaw et al. 2002). Light availability also influences establishment (Coates 2002). Biomass partitioning changes during acclimation following release of the already established trees, and soil and light conditions strongly influence tree growth response (Claveau 2002, Kneeshaw et al. 2002). The acclimation response reflects growth performance prior to release, which in turn reflects pre-release environmental conditions.

Needle-mass variables have been related to growth and acclimation as relative or absolute values. Reich et al. (1998) demonstrated tree acclimation to shading based on relative morphological variables. Leaf morphology was strongly correlated with variation in relative growth rate. Previous tree growth can be used as an attribute for growth projection in empirical individual-tree growth models (e.g., Pukkala and Kolström 1991). Although increment data from tree rings or repeated measurements reflect the growth conditions and history, because of the many factors that affect advance regeneration, there is much unexplained variation in currently available models of advance regeneration.

Norway spruce (*Picea abies* (L.) Karst.) is a shade-tolerant species that can exist as advance regeneration beneath the canopy of a mature forest stand (Jeansson et al. 1989, Lundqvist and Fridman 1996, Valkonen et al. 1998). Our objective was to study the recovery of advance regeneration of Norway spruce after the removal of canopy trees. Specifically, we determined whether variations in sapling structure and competition could explain the rate of recovery of sapling growth after release. The hypotheses tested were: (1) the developmental history of the understory saplings as described by their current size and growth rate affects their growth rates after release; (2) competition reduces the growth of advance regeneration following release; and (3) greater needle mass indicates greater physiological production capacity and induces faster tree growth after release.

Materials and methods

We studied recovery of advance regeneration of Norway spruce trees in three permanent sample plots in the Järvselja Experimental Forest of the Estonian Agricultural University. Järvselja, located in the southeastern part of Estonia (58°25′ N, 27°46′ E) in Tartu county near Lake Peipsi, which is in a temperate zone with a moderately cool and moist climate. Mean annual temperature is 4–6 °C. Annual precipitation is between 500 and 750 mm, about 40–80 mm of which falls as snow. The length of the growing period (daily air temperature above 5 °C) is generally between 170 and 180 days.

The permanent sample plots were located on sandy soils. Plot 1 was established in 1997. In 2000, two more plots (2 and 3) were established in different places and conditions to collect more data. Plot 1 was established on clear-felled area cut in winter 1995–1996. The size of the clear-cut was 2.5 ha. The site type is *Oxalis–Myrtillus* and the site index is bonitet 1. The old canopy (determined by basal area in all plots) consisted of 70% Norway spruce, 20% silver birch (*Betula pendula* Roth) and 10% trembling aspen (*Populus tremula* L.). The volume of the stand before clear-cutting was 338 m^3 ha^{-1}. Stand structure was irregular, with some gaps in the canopy. As a result, the advance regeneration was distributed in patches over the clear-cut area. Advance regeneration trees were sampled in two patches: the first, a dense group under previous heavy shade, the second in a canopy gap. The patches were 40 m apart.

Plot 2 was established in a clear-felled area cut in winter 1999–2000. The size of the clear-cut was 1.1 ha. The site type is *Oxalis–Myrtillus* and the site index is bonitet 1. The main canopy was dominated by Norway spruce (90%) and Scots pine (*Pinus sylvestris* L.) (10%). The volume of the stand before clear-cutting was 288 m^3 ha^{-1}. Most of the advance regeneration trees were located in one large group, but 15 trees were distributed in a second group. These trees were included in the final sampling set.

Plot 3, comprising a stand of 0.6 ha, was situated next to Plot 1, but beneath a dense canopy cover. The site index is bonitet 1 and the site type is *Oxalis–Myrtillus*. The old canopy consisted of 60% Norway spruce, 30% trembling aspen and 10% silver birch. The volume of the stand is 329 m^3 ha^{-1}. The advance regeneration was unevenly distributed in variously sized groups, with trees in various height classes. The overstory of the stand has not been removed, but clear-felling is scheduled for winter 2004–2005.

Plot size and configuration varied during data collection. Plot size was adjusted to accommodate 100 trees. Plots were located in the groups of advance regeneration trees. All trees within the plot perimeter were measured to include the competition effects. In cases where the group exceeded 100 trees, only a sub-area of the group was sampled, but in this case, the trees neighboring sample trees, even though they fell outside the sample plot, but were were within a 2-m radius of the sampled trees, were also measured. Additional trees were selected if the group contained less than 100 trees, which accounts for the separate groups. The trees were numbered and mapped. The number of trees on plots included in the final analysis varied, depending on how many trees survived until the end of observation period, at which time there were 87, 73 and 52 trees left in Plots 1, 2 and 3, respectively.

In addition, coordinates were determined for advance regeneration other than Norway spruce, which was within a 2-m radius around the sample tree. These were trees taken into account when calculating competition index.

Measurements on advance regeneration trees were made at the end of each growing season and included tree height, diameter at root collar, living crown base, crown diameter in two directions (the widest and the direction perpendicular to it) and length of the top shoot (leader). The height of the first living branch of the stem was considered equivalent to the crown base. Variables and units are listed in Table 1.

At each measurement, a lateral shoot was sampled randomly from the upper third of each tree crown. Visual criteria were applied to ensure that no damaged shoots or any with extreme growth were included in the sampling (shoots with signs

Table 1. Variables and units used in the study.

Variable	Symbol	Unit
Tree height	H	cm
Tree diameter at root collar	D	cm
Living crown base	LCB	cm
Top shoot length	TL	cm
Shoot length	L	cm
Needle mass of shoot	M	Mg
Tree basal area (at ground level)	G	mm^2
Tree basal area increment (at ground level)	i_g	mm^2 $year^{-1}$
Competition index	K	–

of browsing were excluded). The shoots and needles collected were assumed to reflect the growth capacity of the tree during the previous year. Excised shoots were taken to the laboratory where shoot length was measured and the number of needles counted. Needles were dried at 70 °C for 72 h and then weighed.

Trees on Plot 1 were destructively sampled after 5 years of growth in full light. Basal discs were removed and tree rings were measured with WinDENDRO (Regent Instruments, Canada) (the width of each growth ring was measured and averaged from two radii).

An index of competition was calculated for each tree as:

$$K = \sum_{k=1}^{N} \frac{H_k}{H_0} \frac{1}{S_k} \tag{1}$$

where K is the competition index, H_k is height of the competitor tree, H_0 is height of the tree and S_k is distance from the competing tree (Hegyi 1974). Some trees died during the observation period and these data are excluded from the analysis.

We used MS Excel (Microsoft, Redmond, WA) and STATGRAPH and SAS software (SAS Institute, Cary, NC) for all correlation and regression analyses. Growth dependencies over the years were subjected to simple regression analysis. Regression equations were fitted for different combinations of variables to obtain the best growth predictions. Tree increment

Table 2. Combination of plot data to demonstrate acclimation processes (years are indicated according to acclimation time and plot no.). Year indicates the observation year (i.e., the previous year was also covered by the data).

Plot	Year after clear-cut					
	0	1	2	3	4	5
1	–	1996	1997	1998	1999	2000
2	–	–	–	2002	2003	–
3	2003	–	–	–	–	–

Table 3. Characteristics of advance regeneration Norway spruce trees.

Plot	Year	Tree height (cm)			Tree diameter (cm)		
		Mean	Min	Max	Mean	Min	Max
1	1996	137	36	352	2.5	0.6	7.3
	1997	156	37	420	2.8	0.7	8.8
	1998	179	38	488	3.4	0.7	7.3
	1999	206	48	418	3.8	1.0	8.3
	2000	227	46	489	4.3	1.0	9.9
2	2001	261	62	630	4.4	1.3	9.0
	2002	315	70	710	5.2	1.4	12.0
	2003	352	80	770	6.2	1.7	12.6
3	2002	159	60	310	2.4	1.1	4.6
	2003	158	55	330	2.7	1.2	5.0

Table 4. Sample shoot characteristics of Norway spruce advance growth trees.

Plot	Year	Needle mass (g)			Shoot length (cm)		
		Mean	Min	Max	Mean	Min	Max
1	1996	0.40	0.02	1.29	9.4	2.0	20.7
	1997	0.39	0.05	1.26	9.2	1.9	29.0
	1998	0.49	0.05	1.83	12.4	2.5	33.8
	1999	0.37	0.06	1.11	11.6	3.4	29.0
	2000	0.57	0.07	1.73	13.4	2.0	37.8
2	2001	0.41	0.14	1.03	10.9	3.5	18.3
	2002	0.77	0.08	1.80	18.3	1.5	33.4
	2003	0.81	0.10	1.81	20.5	2.7	36.5
3	2002	0.19	0.05	0.41	8.4	3.7	14.2
	2003	0.13	0.03	0.40	5.9	2.6	13.2

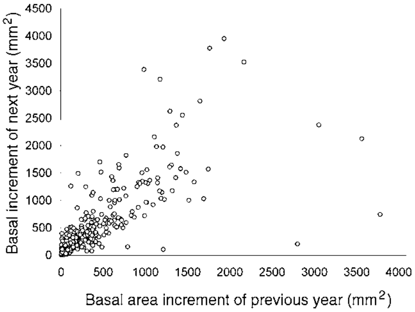

Figure 1. Basal area increment relationship between consecutive years.

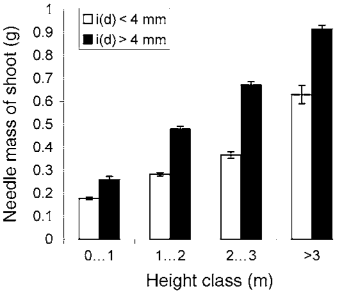

Figure 2. Relationship between tree height class and shoot needle mass. Abbreviation: i(d) = diameter increment.

was related to the previous increment and needle mass. Effects of tree size and competition on growth, with increment and height class as the two factors, were evaluated by two-way analysis of variance (ANOVA) (SAS GLM procedure, SAS Institute). Data from the plots were combined to produce the series for time elapsed since release from the old canopy (years 0–5). Table 2 summarizes how the data were combined to analyze the growth variables. Multiple regression analysis involving transformation of variables was used to describe relationships between tree size and growth in consecutive years, the aim being to predict basal area increment after clear-cutting on the basis of needle and tree characteristics.

The regression model was fitted for the increment function ($n = 457$, $R^2 = 0.81$, RMSE = 0.70):

$$\ln i_{g(t+1)} = a_0 + a_1 \ln i_{g(t)} + a_2 K_t + a_3 \ln g_t + a_4 \ln m_t \qquad (2)$$

where i_g is basal area increment, K_t is competition index at time t, g is basal area at ground level and m_t is needle mass of shoots from the upper third of the tree crown at time t.

Table 5. Summary of two-way ANOVA of the influences of tree size and increment on needle mass.

Source	DF	Sum of squares	Mean square	F value	$P > F$
Model	7	43.479	6.211	93.79	< 0.0001
Error	612	40.532	0.066	–	–
Corrected Total	619	84.011	–	–	–

Results

The basic characteristics of the sample advance regeneration trees are shown in Table 3. Variations in tree dimensions were quite high, as also indicated by the means and variation ranges of the measurements made on sampled shoots (Table 4).

Figure 1 shows the relationship between basal area increments of consecutive years. Some trees damaged by forestry operations or big game exhibited an abrupt drop in growth. Because both ring counting and measurement of ring widths of

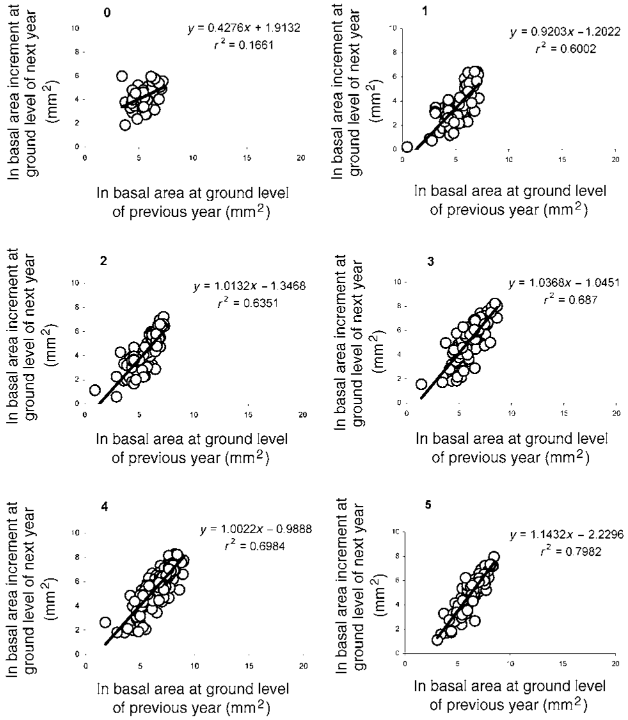

Figure 3. Dependence of basal area growth on tree size (basal area measured at ground level). The bold-face number in each panel denotes the number of years after clear-cutting.

suppressed trees are complicated (Niklasson 2002), errors cannot be entirely excluded; however, the relationship demonstrates increasing growth between consecutive years after clear-cutting.

To model tree height as a function of tree diameter, a regression model of the following type was fitted ($r^2 = 0.89$):

$$h = 56.599d \tag{3}$$

where h is tree height and d is tree diameter at ground level.

Previously, Jõgiste and Metslaid (2002, data not shown) found correlations between shoot needle mass and other shoot characteristics of consecutive years, and the strongest correlation was between shoot length and needle mass. Needle mass of the shoot is considered the most important indicator because it integrates the acclimation of needle size, number and shoot length into a single factor.

Relationships between tree height class and shoot needle mass are shown in Figure 2. Both increment and height class relationships were significant ($R^2 = 0.511$ and $P < 0.0001$; Table 5). When we tried the model for the combined effect of both factors, R^2 increased only to 0.52. Bigger trees tended to have bigger shoots, but in similar-sized trees (same height class) those with larger diameter growth also had greater foliage mass. Both of these variables were highly significant, indicating a correlation between shoot properties and sapling growth.

Relationships between basic variables are presented as regression models. Figure 3 illustrates the relationships between tree increment and tree size, and Figure 4 shows the dependence of basal area growth between consecutive years. A gradual increase in r^2 was observed. There was a tendency for growth to accelerate especially as a function of size. The growth relationships showed more variation, largely because the growth data were combined from several plots (see Table 2).

A similar pattern was seen in the relationships between shoot needle mass and sapling basal area growth in the following year (Figure 5). Linear models provided a simple description of the growth dynamics. Although the dry period in 1999 probably caused reduced growth in the fourth year under full-light conditions, the relationship was nonlinear for certain periods (Figure 5, year 2).

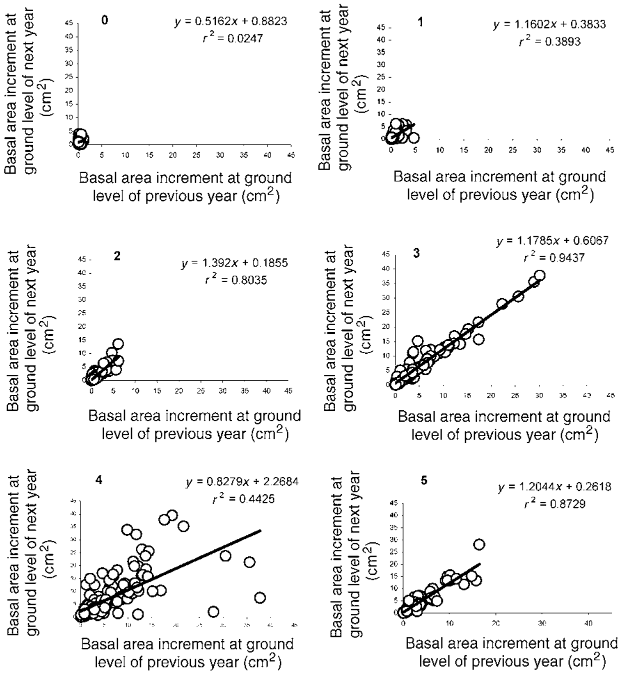

Figure 4. Dependence of basal area growth on the previous year's based growth. The bold-face number in each panel denotes the number of years after clear-cutting.

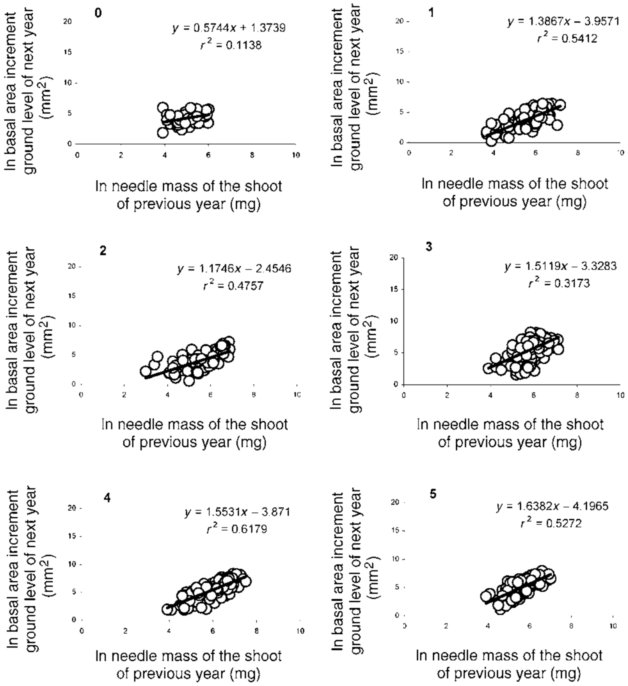

Figure 5. Relationships between basal area growth and shoot needle mass. The bold-face number in each panel denotes the number of years after clear-cutting.

The multiple regression model produced a good prediction for growth (Table 6). We also considered the influences of tree, plot and year in the regression models using dummy variables. Neither the tree and nor the plot influence was significant. Tree, sample plot and year were not significant in the model ($P > 0.05$).

Table 6. Parameter estimates and associated statistics for the logarithm of the basal area increment model in the next year ($t + 1$). Abbreviations: $\ln i_{g(t)}$ is logarithm of basal area increment of the previous year; K_t is competition index in the previous year; $\ln g_t$ is logarithm of basal area of the previous year; and $\ln m_t$ is logarithm of needle mass of the previous year.

Variable	Coefficient	Value	SE	P value
Intercept	a_0	−0.064	0.340	0.851
$\ln i_{g(t)}$	a_1	0.532	0.044	< 0.005
K_t	a_2	−0.014	0.003	< 0.005
$\ln g_t$	a_3	0.280	0.055	< 0.005
$\ln m_t$	a_4	0.188	0.062	< 0.005

The competition influence (Figure 6) showed that both tree size and distance from competitor are significant. The influence of competition was greater in the smaller height classes than in the larger height classes. Trees with smaller competition index values had larger diameter increments.

To predict growth trends that follow from the observations, we simulated the basal area development of saplings according to Equation 2. Because needle mass of the shoot was a variable in the model, we also used the relationships between sapling size, diameter growth and shoot mass to update the shoot characteristics from year to year. Figure 7 shows the simulated growth of trees with three sets of input values, which are described in Table 7. The competition index was constant for all trees during the simulation period. Tree size influenced growth rate to a considerable degree.

Discussion

We investigated basal area increment as a growth variable because it is easy to measure accurately. However, because diameter growth and height growth are correlated, we were able to

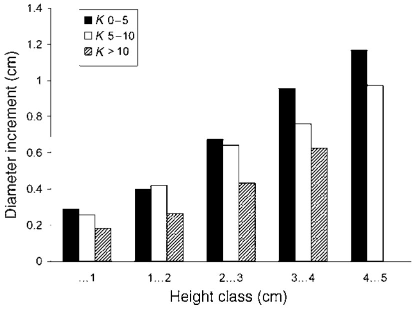

Figure 6. Relationship between height class, diameter increment and competition index (*K*).

use the prognostic value of height increment of the previous year in the model. Height increment has also been used as a mortality predictor (Ruel et al. 1995).

Our model has a qualitative application value. Its diagnostic capacity can be used by forestry practitioners to predict the regeneration success of various size classes. However, the model cannot be used for extrapolations, because we have not yet run the model for canopy trees or for periods longer than 5–6 years after clear-cutting.

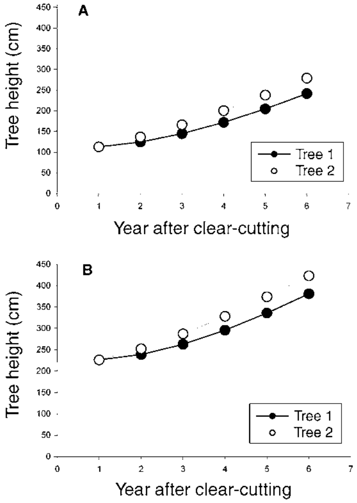

Figure 7. Simulated acceleration in height increment in the absence of competition.

Table 7. Initial values for the model simulations in Equation 2.

	Basal area (mm^2)	Diameter (mm)	Basal area increment (mm^2)	Diameter increment (mm)	Needle mass (mg)	Competition index
A						
Tree 1	314	20	32	0.5	600	0
Tree 2	314	20	66	2	600	0
B						
Tree 1	1256	40	64	0.5	600	0
Tree 2	1256	40	129	2	600	0

Although we did not explicitly estimate the influence of gap size on advance regeneration growth, gap size was present in the analysis because it influenced the initial sapling properties before clear-cutting. Coates (2002) found that tree abundance and species composition appear to be controlled more by differentiation among growth and survival niches than by regeneration niches. Gap size is an important determining factor for tree survival, because growth increment is suppressed in small gaps and only shade-tolerant species can survive until light conditions improve (Messier et al. 1999, Coates 2000). Small gaps are easily closed by the crowns of surrounding trees, creating unfavorable growth conditions for those saplings that gained the most height when the gap opened (Lieffers et al. 1996). In our study, this was manifest as variations in the initial size and growth rate before release and is reflected in sapling performance after the clear-cut (see Figure 7).

We observed that basal area growth was correlated with shoot properties in the upper crown. In similar-sized saplings, basal area growth was more pronounced if the shoots showed vigorous growth, indicating that shoot structure may indicate overall acclimation to the changed conditions. Shoot growth depends on local light conditions, position on the stem and overall tree growth (Nikinmaa et al. 2003). There is evidence that hydraulic limitation also limits shoot growth, but this is likely to be important only in large trees (Koch et al. 2004). Shoots from a similar position in saplings of similar size and growing in similar light conditions are likely to be of similar size. However, following release, the understory saplings are subjected to a major environmental change that influences shoot structure. For example, solar irradiance influences leaf packing on shoots (Niinemets 1997). On the other hand, shoot growth depends on tree growth, especially in Norway spruce, which has a plastic crown structure that is dependent on light conditions. Kneeshaw et al. (2002) observed that understory release causes an immediate growth response in roots but a more gradual response in aerial tree parts. The degree of shoot vigor could indicate the degree of acclimation of the sapling to the new growing conditions. Kneeshaw et al. (2002) also found that larger individuals experienced a greater growth reduction during the first post-harvest growing period than smaller individuals. In our study, although the basal area increment showed a clear tendency to increase in all trees, the timing of growth resumption depended on previous growth.

We found that competition slowed sapling recovery. Lundqvist and Fridman (1996) concluded that competition likely begins around breast height in uneven-aged Norway spruce stands, which is also the size range of the advanced regeneration in our study. Competition eventually leads to self-thinning (Ray et al. 1999). Because understory saplings often occur in patches that have established in previous canopy openings, our results suggest that sapling recovery after release could be accelerated by sapling density control in the patches.

A practical implication of our model of advance growth is the need to tend dense groups. Gap development creates a situation in which trees of different acclimation and development status occur in clumps. The most viable trees in these dense patches can be identified based on previous growth (both lateral and leader lengths), foliage abundance and tree size. The tallest trees with a high needle mass should be identified as crop trees and competition by other advance growth and deciduous trees removed.

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Erialane enesetäiendamine

2006	Tudeerimine Helsingi ülikooli metsaökoloogia osakonnas. Soome

2006	Metsa uuendamine boreaalsete ja laialeheliste lehtpuumetsade vööndis. Kursuse organiseerija: Rootsi Põllumajandusteaduste ülikool Alnarpis. Rootsi
2006	Säästev metsamajandus. Kursuse organiseerija: Helsingi ülikooli metsaökoloogia osakond. Soome
2006	Boreaalsete metsade struktuur, dünaamika ja looduslik mitmekesisus. Kursuse organiseerija: Helsingi ülikooli metsaökoloogia osakond. Soome
2005	Riiklikud metsandusprogrammid arengumaades. Kursuse organiseerija: Helsingi ülikooli metsaökoloogia osakond. Soome
2005	Tudeerimine Helsingi ülikooli metsaökoloogia osakonnas. Soome
2004	Metsanduslike arengustsenaariumite modelleerimine. Kursuse organiseerija: Leedu Põllumajandusülikool Kaunases. Leedu

Projektid

2008	Sihtfinantseeritav teema SF0170014s08: “Muutuvate kliimatingimuste mõju boreaalse ja parasvöötme metsade häiringurežiimile”, täitja
2003-2008	“Tormikahjustuste ja metsapõlengute majanduslik ja ökoloogiline hindamine Eesti metsades” (SA Keskkonnainvesteeringute Keskus), täitja
2003-2007	Sihtfinantseeritav teema SF0432486s03: “Looduslike häiringute ja inimtegevuse mõju metsaökosüsteemide dünaamikale ja mitmekesisusele”, täitja
2003-2007	“Häiringute analüüs metsaökosüsteemide majandamises” (Põhjamaade Ministrite Nõukogu, Põhjamaade Metsanduslik Uurimiskomitee), täitja
2000	“Kuuse-kase segapuistu kasvudünaamika uurimine püsikatse meetodil” (Keskkonnaministeerium), täitja

Teadustöö põhisuunad

Teadustöö on keskendunud metsade loodusliku uuenemise aspektidele. Okaspuu loodusliku uuenduse kasutamine metsade majandamisel Eestis.

Võõrkeelte oskus

Inglise, vene, soome, leedu

LIST OF PUBLICATIONS

Publications indexed in the ISI Web of Science database

Metslaid, M., Jõgiste, K., Nikinmaa, E., Moser, W.K. and Porcar-Castell, A. 2007. Tree variables indicating the growth response and acclimation of advance regeneration of Norway spruce and other coniferous species after the release. Forest Ecology and Management 250, 56-63.

Ilisson, T., **Metslaid, M.,** Vodde, F., Jõgiste, K., Kurm, M. 2006. Vascular plant response to windthrow sverity in Norway spruce dominated *Myrtillus* site type forests in Estonia. Ecoscience 13, 193-202.

Metslaid, M., Ilisson, T., Nikinmaa, E., Kusmin, J., Jõgiste, K. 2005. The recovery of advance regeneration after disturbances: acclimation of needle characteristics in *Picea abies*. Scandinavian Journal of Forest Research. 20 (Suppl. 6), 112-121.

Ilisson, T., **Metslaid, M.,** Vodde, F., Jõgiste, K., Kurm, M. 2005. Storm disturbance in forest ecosystems in Estonia. Scandinavian Journal of Forest Research 20 (Suppl. 6), 88-93.

Metslaid, M., Ilisson, T., Vicente, M., Nikinmaa, E., Jõgiste, K. 2005. Growth of advance regeneration of Norway spruce after clear-cutting. Tree Physiology 25, 793-801.

Papers in Estonian and in other peer-reviewed research journals with a local editorial board

Metslaid, M., Jõgiste, K. and Nummert, K. 2007. Net photosynthesis as indicator of acclimation of Norway spruce advance regeneration. Miškininkyste 1 (61), 20-24.

Metslaid, M., Ilisson, T., Jõgiste, K. 2005. Hariliku kuuse eeluuenduse kasvumudel lageraie järgselt (A growth model of advance regeneration of Norway spruce after clearcut). EPMÜ Metsandusteaduskonna toimetised (Transactions of the Faculty of Forestry, Estonian Agricultural University) 38, 46-52.

Ilisson, T., Repo, M., Jõgiste, K., **Metslaid, M.** 2005. Tormikahjustuse iseloomu mõjutavad tegurid Tudu ja Halliku metskonna katsealadel (Factors influencing storm damage in sample areas of the Tudu and Halliku forest districts). EPMÜ Metsandusteaduskonna toimetised (Transactions of the Faculty of Forestry, Estonian Agricultural University) 38, 30-37.

Metslaid, M., Ilisson, T., Nikinmaa, E., Jõgiste, K., Kiviste, A. 2004. The advance regeneration after disturbances: acclimation of Norway spruce by needle characteristics. Proceeding of the International Conference 'Natural Disturbances and Ecosystem-Based Forest Management.' Tartu, Estonia. 27-29 May 2004. 71-74.

Ilisson, T., **Metslaid, M.,** Jõgiste, K. 2004. Storm as a disturbance factor in forest ecosystems: Tudu and Halliku case study. Proceeding of the International Conference 'Natural Disturbances and Ecosystem-Based Forest Management.' Tartu, Estonia. 27-29 May 2004. 104-107.

Jõgiste, K. & **Metslaid, M.** 2002. Acclimation of spruce advance regeneration to light conditions: estimation by needle characteristics. Forestry studies 36, 26-31.

Kari, I., Jõgiste, K. & **Metslaid, M.** 2002. Kuuse eeluuenduse kasv sõltuvalt kohanemisest lageraie järgselt (The growth of spruce advance regeneration depending on acclimation after clearcutting). EPMÜ metsandusteaduskonna toimetised (Transactions of the Faculty of Forestry, Estonian Agricultural University) 35, 43-49.

Abstracts

Köster, K., **Metslaid, M.,** Jõgiste, K. and Ilisson, T. 2007. Species influence to the mechanism of wind damage in mixed stands. Proceeding of the International Conference 'Wind and Trees.' Vancouver, Canada, 5-9 August, 2007. pp. 83.

Metslaid, M. and Jõgiste, K. 2006. Acclimation on Norway spruce advance regeneration after release cuttings. Proceeding of the International Conference 'Natural disturbaance-based silviculture: Managing for complexity.' Rouyn-Noranda, Canada, 14-18 May, 2006. pp. 217-221.

Jõgiste, K., **Metslaid, M.,** Ilisson, T. 2006. The wind disturbances and regeneration patterns in Norway spruce forest in Estonia. Proceeding of the International Conference 'Natural disturbaance-based silviculture: Managing for complexity.' Rouyn-Noranda, Canada, 14-18 May, 2006. pp. 86-88.

Metslaid, M., Ilisson, T., Vicente, M., Nikinmaa, E., Jõgiste, K. 2004. Growth of advance regeneration of Norway spruce after clearcut: model analysis. In: Hasenauer, H. & Mäkelä, A. (eds.). Modeling forest production. Proceedings of the International Conference held in Vienna, Austria, 19. – 21. April 2004. pp. 274-277.

Ilisson, T., Jõgiste, K., Repo, M., **Metslaid, M.** 2004. The response of undestory vegetation to windstorm at different scale of damage in Norway spruce dominated forests, Estonia. In: Maslov, A.,A. (ed.). Disturbance dynamics in boreal Forests; Abstracts of the V International Conference, Dubna, Russia, August 1 – 5, 2004. pp 24.

APPROBATION

International conferences and meetings

1. 12.12.2007. **Marek Metslaid**, Kalev Jõgiste "Acclimation of Norway spruce and photosynthesis" ("Hariliku kuuse kohanemine ja fotosüntees") suuline ettekanne rahvusvahelisel seminaril "The 1st Tartu – Helsinki workshop" Hyytiäläs (Soomes).

2. 04.10.2007. Kajar Köster, **Marek Metslaid**, Kalev Jõgiste, Kaljo Voolma, Diana Laarmann "Assessment of tree mortality after windthrow using photo-derived data" ("Puude suremuse hindamine foto-tuletatud andmete põhjal") posteri ettekanne rahvusvahelisel konverentsil "Disturbance regimes in changing environment" Tukumsis (Lätis).

3. 06. 08. 2007. Kajar Köster, **Marek Metslaid**, Kalev Jõgiste, Triin Ilisson "Species influence to the mechanism of wind damage in mixed stands" ("Puuliigi mõju tormikahjustuste mehhanismile segametsades") posteri ettekanne kaasautorina rahvusvahelisel konverentsil "Wind and Trees" Vancouveris (Kanadas).

4. 12. 09. 2006. **Marek Metslaid**, Kalev Jõgiste, Kaarel Nummert "Acclimation of advance regeneration of Norway spruce after release" ("Hariliku kuuse eeluuenduse kohanemine vabastuse järgselt") posteri ettekanne rahvusvahelisel konverentsil "Disturbances at the landscape level: ecology and management" Tromsøs (Norras).

5. 15.-16. 05. 2006. **Marek Metslaid**, Kalev Jõgiste "Acclimation of Norway spruce advance regeneration after release cuttings" ("Hariliku kuuse eeluuenduse kohanemine vabastusraiete järgselt") posteri ettekanne rahvusvahelisel konverentsil "Natural disturbance-based silviculture: Managing for complexity" Rouyn-Norandas (Kanadas).

6. 29. 09. 2005. **Marek Metslaid**, Kalev Jõgiste, Eero Nikinmaa, Albert Porcar-Castell "Ecophysiological measurements of acclimation of Norway spruce advance regeneration" ("Hariliku kuuse eeluuenduse kohanemine ökofüsioloogiliste mõõtmiste põhjal") posteri ettekanne rahvusvahelisel konverentsil "The scale of natural disturbances from tree to stand" Palangas (Leedus).

7. 28. 05. 2004. **Marek Metslaid**, Triin Ilisson, Eero Nikinmaa, Kalev Jõgiste, Andres Kiviste “The advance regeneration after disturbances: acclimation of Norway spruce by needle characteristics” (“Eeluuendus häiringute järgselt: hariliku kuuse kohanemine okaste põhjal”) ettekanne rahvusvahelisel konverentsil “Natural Disturbances and Ecosystem-Based Forest Management” Tartus.

8. 19. 04. 2004. **Marek Metslaid**, Triin Ilisson, Marta Vicente, Eero Nikinmaa, Kalev Jõgiste “Growth of advance regeneration of Norway spruce after clearcut: model analysis” (“Hariliku kuuse eeluuenduse kasv lageraie järgselt: mudeli analüüs”) posteri ettekanne rahvusvahelisel konverentsil “Modeling Forest Production” Viinis (Austrias).

Local conferences and meetings

1. 10. 05. 2007. **Marek Metslaid** “Hariliku kuuse eeluuenduse kohanemine ja kasv lageraie järgselt” EMÜ Doktorantide ettekannetepäeval.

2. 24. 05. 2004. **Marek Metslaid** „Hariliku kuuse eeluuenduse kohanemisest lageraie järgselt“ EPMÜ Metsandusteaduskonna seminaril.

3. 22. 04. 2004. **Marek Metslaid,** Triin Ilisson „Hariliku kuuse eeluuenduse kohanemisest lageraie järgselt“ EPMÜ Metsandusteaduskonna magistrantide ja doktorantide ettekannetepäeval (esitas Triin Ilisson).

VIIS VIIMAST KAITSMIST

06.06.2008 kaitses EMÜ Põllumajandus- ja keskkonnainstituudi doktorant **Anu Kisand** väitekirja filosoofiadoktori kraadi taotlemiseks hüdrobioloogia erialal: Sediment phosphorus forms and their role in lake ecosystems / Settefosfori vormid ning nende mõju järvede ökosüsteemidele
Juhendaja: vanemteadur Tiina Nõges.

29.05.2008 kaitses EMÜ Põllumajandus- ja keskkonnainstituudi doktorant **Ruth Lauk** väitekirja filosoofiadoktori kraadi taotlemiseks taimekasvatuse erialal: Theoretical and practical aspects of growing legume-ceral mixes / Kaun- ja teraviljade segukülvide kasvatamise teoreetilisi ja praktilisi aspekte
Juhendaja: prof. Ervi Lauk.

25.04.2008 kaitses EMÜ Veterinaarmeditsiini ja loomakasvatuse instituudi doktorant **Mati Roasto** väitekirja filosoofiadoktori kraadi taotlemiseks veterinaarmeditsiini erialal: *Campylobacter* spp. in poultry and raw poultry meat products in Estonia with special reference to subtyping and antimicrobial susceptibility / Kampülobakterite esinemine Eestis kodulindudel ja tooretes linnulihatoodetes, tüvede tüpiseerimine ja antibiootikumidele tundlikkuse määramine
Juhendajad: prof. Maarja-Liisa Hänninen, prof. Ari Hörman, prof. Priit Elias.

23.01.2008 kaitses EMÜ Metsandus- ja maaehitusinstituudi doktorant **Raul Rosenvald** väitekirja filosoofiadoktori kraadi taotlemiseks metsanduse erialal: Biota and persistence of retention trees in relation to the characteristics of the trees and cut areas / Säilikpuude elustikuja säilivuse seosed raiesmiku ja puu omadustega
Juhendajad: prof. Hardi Tullus, vanemteadur Asko Lõhmus.

11.12.2007 kaitses EMÜ Põllumajandus- ja keskkonnainstituudi doktorant **Helen Agasild** väitekirja filosoofiadoktori kraadi taotlemiseks hüdrobioloogia erialal: The role of zooplankton grazing in shallow eutrophic lake ecosystems / Zooplanktoni toitumise mõju madalate eutroofsete järvede ökosüsteemile
Juhendaja: vanemteadur Tiina Nõges.

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