Regeneration Process from Seed Crop to Saplings – a Case Study in Uneven-Aged Norway Spruce-Dominated Stands in Southern Finland

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The dynamics of spruce regeneration, from seed crop to saplings, was studied based on five permanent plots in uneven-aged, spruce-dominated, boreal forest stands, cut with single-tree selection in the beginning of the 1990's. The annual fluctuation of the spruce seed crop was very similar in uneven-aged and even-aged stands. The correlation between seed crop and number of germinants was significant; but stem number, basal area or volume of the stand did not influence on seedling emergence. The effects of good seed crops were seen as peaks or an increase in the number of germinants and smallest seedlings. The mean number of 'stabilised' spruce seedlings (height 11 cm to 130 cm) varied from 6000 ha^{-1} to over 25 000 spruce seedlings ha^{-1} from one monitoring plot to another. On a monitoring plot the number of 'stabilised' spruce seedlings was stable over time. Neither stand basal area nor stand volume influenced the number of 'stabilised' spruce seedlings, but the height of these seedlings was higher on subplots with lower stand volume and smaller basal area. In this study the monitoring period, 5–10 years, was too short to obtain reliable figures for ingrowth, i.e. the transition of seedlings to the sapling stage (h > 130 cm). The adjusted mean ingrowth was 26 stems ha^{-1} year^{-1}.

Keywords uneven-aged, boreal forest, *Picea abies*, regeneration
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1 Introduction

One of the key elements in sustainable forest management is successful forest regeneration. In uneven-aged forest management, where the regeneration process should be more or less continuous, the recruitment of new trees is especially important. Regeneration processes in even-aged forest management are fairly well known, and regeneration methods are highly developed. Moreover, detailed handbooks on regeneration procedures for the clear cutting system are available, e.g. Grossnickle (2000). The regeneration processes in uneven-aged boreal forests are not so well known (e.g. Nilson and Lundqvist 2001), and measures for promoting regeneration in an uneven-aged (uneven-sized) and/or multilayered stand are not so familiar to practical foresters.

The abundance of seed crop and the factors affecting the quantity and quality of seed crops have been studied and monitored for a long time in Finland, e.g. by Heikinheimo (1932, 1937, 1949), Sarvas (1952, 1962,1968) and Hokkanen (2000), as well as in Sweden, e.g. by Tirén (1935) and Andersson (1965). Variation in seed crop between years, areas, stands and trees has been very pronounced for conifers in boreal forests, especially for Norway spruce (*Picea abies* (L) Karst.).

In southern Finland good cone years for spruce have occurred three to four times in ten years. But, within the same ten-year period, the five-year result might have been a very poor seed crop. Even if a cone year happens to be good, the seed crop may be almost totally destroyed by seed pests (Hokkanen 2000).

Although some seed will be available almost every year, the emergence of new germinants is not guaranteed. The most critical factors in the germination process are seedbed quality and weather conditions during the germination phase. In a wet summer, first-year seedlings can also be found on unfavourable seedbeds where they have no possibilities to grow further; on the contrary, dry and warm weather during the growing season strongly decreases germination (e.g. Yli-Vakkuri 1961, Valkonen 1996, de Chantal 2003).

The first years after germination are difficult for small seedlings. In the first years the annual mortality may be as high as 90% (Arnborg 1947, Leemans 1991). In the beginning, the crucial component is the competition for water between the seedlings and the ground vegetation. A few years later, the competition with ground vegetation, shrubs and trees for light will play an increasing role in the seedlings' struggle for life. When the seedlings have reached a height of about 10 cm, the probability of survival is much higher than earlier and development of the seedling population is more stable and easier to predict. The annual mortality rates of such seedlings are generally about 3 to 10% (Lundqvist 1991, Nilson 2001). Since regeneration on the whole is the result of a chain of lucky events, new trees often enter the tree stand in cohorts (Oliver and Larsson 1990, Kolström 1992).

The aim of this study was to describe the variation in seed crop and seedling emergence in different years. Furthermore, the dynamics of seedling establishment in an uneven-aged boreal forest will also be analysed. The empirical background of the study comes from permanent plots established in uneven-aged, spruce-dominated, boreal forest stands in southern Finland.

2 Materials and Methods

In the beginning of the 1990's five stands that already had an uneven structure were chosen for the study. The uneven structure was seen at least in the tree size distribution; the tree ages were not determined (Fig. 1). These stands were each about 2 ha in area and were all spruce-dominated. They were situated in southern Finland (N 61º00'–62º30', E 25º00'–27º30') on mineral soils, and the forest site type was either *Oxalis-Myrtillus* or *Myrtillus* type, classified according to the definitions of Cajander (1949).

In 1992–1994, monitoring plots were established in these stands. On a monitoring plot (80 m × 100 m in area) all trees $h > 1.3$ m were mapped and measured for diameter ($d_{1.3}$), height and crown length. With the remeasurements, made 5 and 10 years after the establishment, new trees (saplings that entered the 1.3 m dbh level between the successive measurements) were recorded. These monitoring plots were

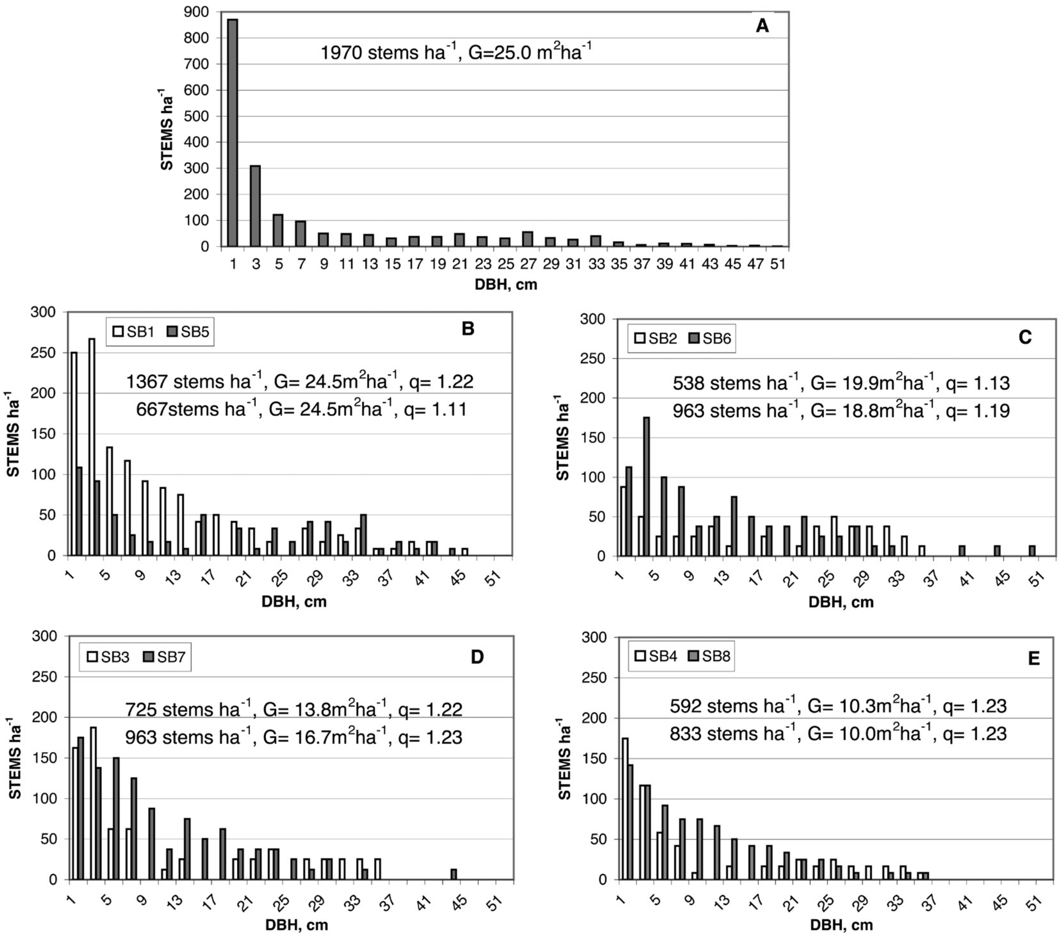

Fig. 1. An example of stem distributions (dbh) in one field experiment (Vesijako). In subpicture A the overall stem distribution on all subplots before single-tree selection cutting. In subpictures B–E the stem distributions after single-tree selection cutting on eight subplots (SB1 to SB8). Stem distributions on subplots with same target basal area are in the same subpicture.

each divided into eight subplots with four different basal area levels (after single-tree selection), either 8, 12, 16 and 20 m^2 ha^{-1} (field experiments Vesijako and Mikkeli) or 10, 15, 20 and 25 m^2 ha^{-1} (field experiments Suonenjoki I, II and Evo) (Fig. 2, see also Valkonen 1996). These subplots were systematically distributed into two opposed rows on the monitoring plot with buffer zones between rows (see Fig 2).

The trees to be removed were marked with the help of a computer program. First all sick trees and trees with defects were marked for removal. Then, for the rest of trees to be removed, the main aim in the marking process was to decrease the competition from bigger trees in favour of smaller ones, taking into account the target basal area and q-value (Table 1). The q-values were determined using a 2-cm class width in dbh-distribution. After cuttings, the proportion of spruce varied from 68% to 94% (basal area). After cuttings the uneven structure was still present or was even more pronounced than before cutting (Fig. 1).

Five years after cutting the average basal area on the monitoring plots was 22–25 m^2 ha^{-1} (varying on the subplot level from 12 to 36 m^2 ha^{-1} (Table 1)). The variation in stand volume was

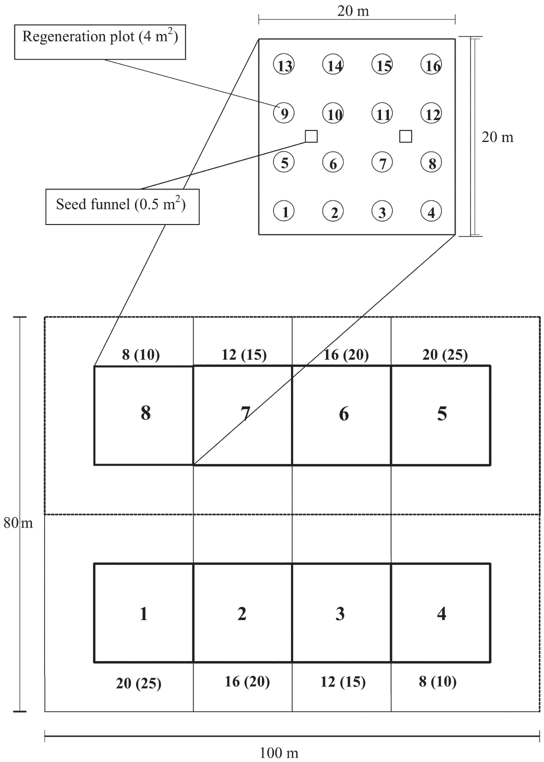

Fig. 2. Experimental design on one monitoring plot having eight subplots with different stand basal areas. The plot grid used in regeneration measurements and seed funnels in one subplot as an example.

even larger, 100 m^3 ha^{-1} to 410 m^3 ha^{-1} (between subplots). In the Mikkeli field experiment the mean stand volume was lowest, 184 m^3 ha^{-1}; in other field experiments the mean stand volumes were 210–260 m^3 ha^{-1} (see Table 5).

Two seed funnels (trap area 0.5 m^2) were placed systematically in every subplot (16 seed funnels in every monitoring plot). Seeds were collected from these funnels at least four times between the beginning of April and the end of November. Seeds were dried and extracted from the forest litter, and the full seeds were counted according to tree species. The number of full seeds was converted to weight (g ha^{-1}) with the help of the funnel trap area and the seed weights found in the literature: 200 seeds g^{-1} for pine (*Pinus sylvestris*), 250 seeds g^{-1} for spruce and 4000 seeds g^{-1} for birches (*Betula pendula* and *B. pubescens*) (Nygren 2003). The General Linear Model was used to examine the differences in seed crop between basal area levels and seed collection years in each field experiment. In order to obtain equal error variances on the subplot level, the amount of spruce seeds was ln-transformed.

Seedlings (h < 1.3 m) on each subplot was monitored using sixteen 4 m^2 circular plots in a 5 m × 5 m grid (Fig 2.). Heights of the observed seedlings were measured and tree species determined late in the autumn of every year throughout

Table 1. Basal area in experimental stands (trees taller than 1.3 m) by subplots before cutting (B), after cutting (A0) and five years after cutting (A5).

Experimental stand	Basal area in different subplots, m^2 ha^{-1}	1.	2.	3.	4.	5.	6.	7.	8.
Vesijako	B.	33.1	25.4	33.3	28.0	28.8	23.1	24.3	24.3
q-value:	A0.	24.5	19.9	13.8	10.3	24.5	18.8	16.7	10.0
1.13–1.21	A5	31.8	24.4	20.9	12.5	27.9	24.7	20.6	14.2
Evo	B.	24.2	21.8	21.1	24.2	30.0	27.4	24.9	23.7
q-value:	A0.	23.6	18.9	14.9	9.8	21.3	20.0	13.5	9.8
1.13–1.23	A5.	34.5	28.6	21.9	15.1	31.9	30.4	19.7	14.6
Suonenjoki I	B.	33.1	25.5	33.3	28.0	28.8	23.1	24.3	24.3
q-value:	A0.	24.5	19.9	13.8	10.3	24.5	18.8	16.9	10.0
1.11–1.23	A5.	34.3	27.9	20.0	15.2	35.8	27.9	23.1	15.8
Suonenjoki II	A.	22.6	20.3	23.3	25.4	24.2	22.9	23.5	25.9
q-value:	A0.	9.5	13.8	19.1	18.9	9.7	15.4	19.0	22.2
1.13–1.19	A5.	14.6	20.4	27.0	27.5	14.8	20.9	27.3	33.6
Mikkeli	B.	14.4	18.8	18.8	24.3	9.7	13.5	19.7	26.2
q-value:	A0.	9.8	14.9	18.9	23.6	9.8	13.5	20.0	21.3
1.16–1.38	A5.	15.0	19.4	25.1	28.5	14.5	18.2	21.7	29.8

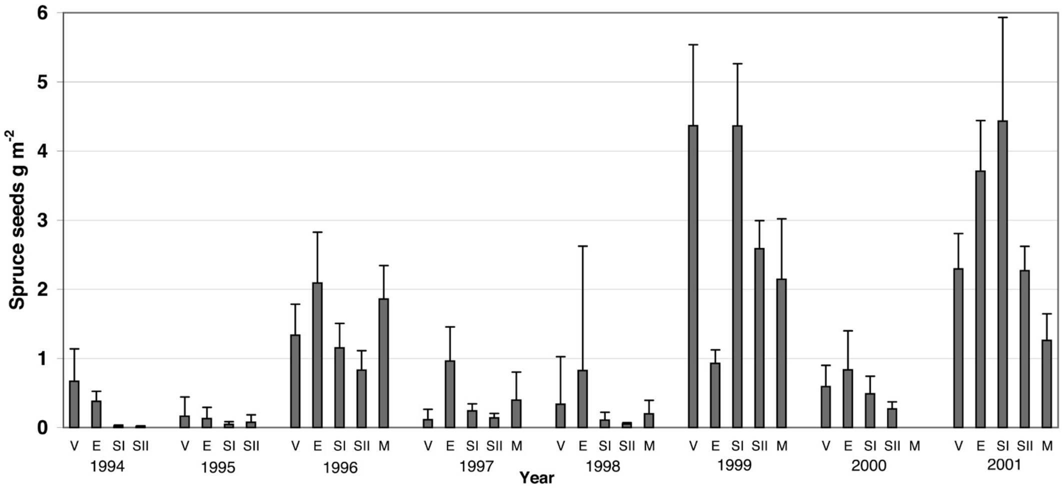

Fig. 3. The observed spruce seed crop on the monitoring plots in years 1994–2001. Standard deviations are marked as a segment on the bars. V = Vesijako, E = Evo, SI = Suonenjoki I, SII = Suonenjoki II, and M = Mikkeli field experiment.

the whole monitoring period, but there was no individual follow-up at seedling level. In data analyses seedlings were classified to the following height classes: germinants (1–2 cm tall seedlings), 'labile' seedlings (3–10 cm tall seedlings), 'stabilised' seedlings (11–50 cm tall and 51–130 tall seedlings). Pearson's correlation coefficients were calculated between stand characteristics and the number of germinants, 'stabilised' seedlings and mean and median height of 'stabilised' seedlings on the subplot level. Height classification was based on tradition used in regeneration studies in Finland (e.g. Sarvas 1944, Leinonen et al. 1989).

3 Results

3.1 Seed Crop

Pine seeds were found on only the two monitoring plots (Suonenjoki I and II) where pine trees composed of 5–9% of the stand basal area. On these monitoring plots the average seed crop of pine varied from 10–20 g ha^{-1} (in 1995) to 1.0–1.5 kg ha^{-1} (in 1999) and the mean values were 250–550 g ha^{-1}.

On all monitoring plots birch seeds were present every year, in 1998 and 2000 the birch seed crop was very abundant, nearly 40 kg ha^{-1}. In other monitoring years it varied from 1.6 kg ha^{-1} to 6.4 kg ha^{-1}.

The spruce seed crop varied considerably among the eight monitoring years (Fig. 3). In years 1994–95, 1997–98 and 2000 the mean annual seed crop for all five monitoring plots was 1.0 to 5.5 kg ha^{-1}. In 1996, 1999 and 2001 it was remarkably higher, 14.5 kg ha^{-1} to 28.8 kg ha^{-1}. Variation in the spruce seed crop between monitoring plots was large; but the three above-mentioned peak years were found in every monitoring plot. Every monitoring plot had some spruce seed every year, and the maximum annual seed crop for one seed funnel was over 80 kg ha^{-1}.

On the same monitoring plot the correlation in seed crops between the subplots with different stand basal areas was evident, and in three monitoring plots the basal area had a statistically significant effect on the seed crop (Table 2). In Suonenjoki I the subplots with lowest basal area had significantly smaller seed crops than the other subplots did. In Mikkeli the subplots with the highest basal area had significantly larger seed crops than the other subplots did.

Table 2. F-values for influence of year (random factor) and level of stand basal area (fixed factor) on the variation of the spruce seed crop on different experimental stands, according to ANOVA. The dependent variable (amount of spruce seeds / subplot / year) was ln-transformed and the combined effect was omitted because there was no significant interaction between year and basal area.

Main effects	Vesijako	Evo	Suonenjoki I	Suonenjoki II	Mikkeli	Overall
Year (random factor)						
F-value	115.4	45.5	321.6	385.9	80.1	127.7
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
df	7/53	7/53	7/53	7/53	4/32	7/287
Basal area level (fixed factor)						
F-value	1.98	6.61	8.64	1.48	10.7	4.82 [1]
p-value	0.127	0.001	0.000	0.229	0.000	0.029
df	3/53	3/53	3/53	3/53	3/32	1/287

1) Exact subplot value of basal area of spruce used as covariate.

Table 3. Pearson's correlation coefficients between the number of spruce germinants and seed crop, basal area, stand volume and stem number on different experimental stands.

Experimental stand		Seed crop (spruce)	Basal area (spruce)	Stand volume	Stem number
Vesijako	correlation	0.244	0.048	0.038	0.080
(n=64)	p-value	0.052	0.706	0.769	0.528
Evo	correlation	0.493	0.214	0.206	0.129
(n=64)	p-value	0.000	0.089	0.102	0.309
Suonenjoki I	correlation	0.433	0.226	0.036	0.474
(n=64)	p-value	0.000	0.072	0.777	0.000
Suonenjoki II	correlation	0.376	–0.081	–0.011	–0.170
(n=64)	p-value	0.002	0.524	0.932	0.178
Mikkeli	correlation	0.545	0.257	0.278	–0.335
(n=40)	p-value	0,000	0.109	0.083	0.035
Overall	correlation	0.261	–0.097	–0.019	0.097
(n=296)	p-value	0.000	0.223	0.749	0.095

3.2 First Year Spruce Seedlings

On every monitoring plot some spruce germinants were observed almost every year (Fig. 4). In the same year, however, the number of new seedlings varied considerably between monitoring plots (coefficient of variation was usually over 100%). Even in a good seed year the number of newly emerged seedlings varied markedly. In 1999, about 1500 new seedlings emerged from 29 kg ha^{-1} of spruce seed (about 7.25 million seeds). In 1996, about 500 new seedlings emerged from the mean seed crop of 15 kg ha^{-1}.

The correlation between germinants (observed in late autumn) and seed crop was significant on four of five monitoring plots (Table 3). Correlations between the number of germinants and the basal area of spruce or stem number or volume of the stand were not significant, except the correlation between stem number and number of germinants in the Suonenjoki I field experiment.

3.3 Seedlings (2 cm < height < 131 cm)

The number of spruce seedlings varied considerably from one monitoring plot to another (Fig. 4). In Vesijako and Evo field experiments the number of spruce seedlings averaged about 6000–10 000 ha^{-1}; in Suonenjoki both monitoring plots

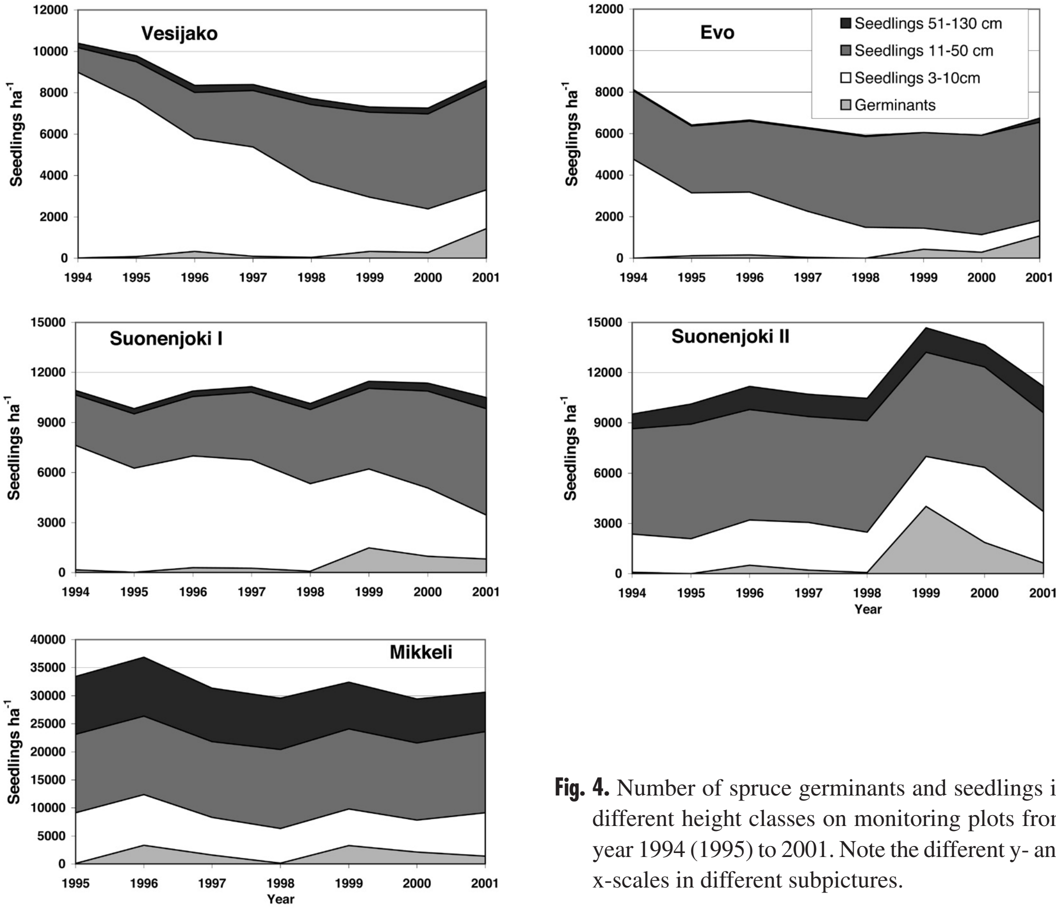

Fig. 4. Number of spruce germinants and seedlings in different height classes on monitoring plots from year 1994 (1995) to 2001. Note the different y- and x-scales in different subpictures.

included 9000–15 000 spruce seedlings ha^{-1}. The Mikkeli field experiment, with the lowest stand volume, had the most abundant spruce regeneration, about 30 000 spruce seedlings ha^{-1}. During the monitoring time the number of germinants and the smallest seedlings, height 3 to 10 cm, varied most. The effects of good seed crops in years 1993, 1996 and 1999 can be seen as 'peaks' in the number of these small, 'labile' seedlings.

Except in Mikkeli field experiment, the number of 'stabilised' spruce seedlings, height 11 to 130 cm, increased during the monitoring time. At the end of the monitoring period, on no monitoring plot, did the number of these seedlings differ from the situation just after cutting. Within the five years (1995–2000), the mean and median height of 'stabilised' seedlings increased on Vesijako and Mikkeli monitoring plots but decreased on Evo and Suonenjoki II.

The correlation between the 'stabilised' seedlings and stand characteristics was low, but the correlation between seedling height and stand characteristics was statistically significant (Table 4). The stem number had a positive effect on the height of the seedlings, while both basal area and stand volume had a negative effect on seedling height. The change in seedling height from 1995 to 2000 was not correlated with any of the stand characteristics measured.

The number of tallest seedlings, height over 50 cm, was very small compared to the smaller height classes (except in Mikkeli). In the Evo field experiment there were hardly any tall seedlings; in Vesijako and Suonenjoki I and II field experiments the number of tall seedlings varied from 200 to 1000 seedlings ha^{-1}. In the Mikkeli field experiment almost one third of seedlings (about 7500 ha^{-1}) belonged to the tallest seedling class.

Table 4. Pearson's correlation coefficients between the mean and median heights of 'stabilised' seedlings (height ranging from 11 cm to 130 cm) and basal area, stand volume and stem number (n=40).

		Stem number	Basal area	Stand volume
Number of stabilised seedlings (2000)	correlation	0.400	–0.172	–0.265
	p-value	0.011	0.288	0.099
Mean height (2000)	correlation	0.459	–0.546	–0.619
	p-value	0.003	0.001	0.000
Median height (2000)	correlation	0.379	–0.459	–0.515
	p-value	0.016	0.003	0.001
Change in mean height (1995–2000)	correlation	–0.066	0.069	0.109
	p-value	0.684	0.672	0.504
Change in median height (1995–2000)	correlation	–0.140	0.062	0.112
	p-value	0.390	0.702	0.492

Table 5. Stem number (all trees with h > 1.3 m) five years after single tree selection cutting and the number of new spruce saplings (height > 1.3 m) in the first and the second five year period after single tree selection cutting.

	Stand volume, m^3 ha^{-1} Mean (min-max)	Stems, ha^{-1} Mean (min-max)	Number of new saplings (h > 1,3m), ha^{-1} The first 5-yrs	The second 5-yrs
Vesijako	210 (102–319)	1508 (1233–1933)	79	75
Evo	263 (143–384)	889 (711–1133)	12	6
Suonenjoki I	260 (137–413)	1322 (900–1867)	113	117
Suonenjoki II	241 (147–338)	1665 (1056–2711)	67	342
Mikkeli	184 (105–293)	1893 (1367–3000)	1076	*
Mean	232 (102–413)	1455 (711–3000)	268 (86)**	135 (178)**

* Second measurement in autumn 2004
** Mean value of Vesijako, Suonenjoki I and II

In the Mikkeli field experiment, where spruce regeneration was most abundant, over 90% of inventory plots (4 m^2) had spruce seedlings. On other monitoring plots about 20–45% of the inventory plots were without spruce seedlings, and seedlings over 50 cm tall were found on every tenth survey plot.

3.4 From Seedlings to Saplings

The transition of seedlings to saplings (height over 1.3 m) varied considerably between monitoring plots (Table 5). In the Evo field experiment within the five year period there were only 6–12 new spruce saplings ha^{-1} (about 1% of the number of stems). During that period, in Vesijako and in Suonenjoki I and II field experiments the number of new saplings varied from 67 to 342 ha^{-1} (5–20% of the number of stems). In the Mikkeli field experiment the transition from seedlings to saplings in the first 5-year period was over tenfold compared with the other monitoring plots. If the minimum (Evo) and the maximum (Mikkeli) values are not included, the average transition from seedlings to saplings was 260 stems ha^{-1} in ten years.

4 Discussion

In uneven-aged forest stands the seed source, mature trees, is always present. The seed crop of conifers, i.e. pine and spruce, has an annual fluctuation as a function of climatic and weather

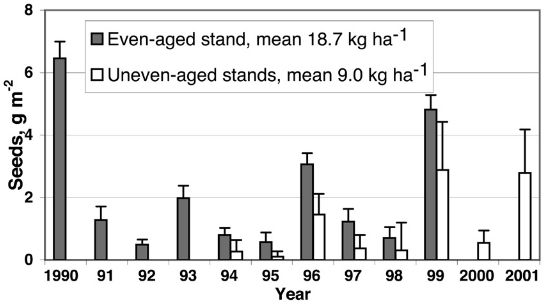

Fig. 5. Spruce seed crop in uneven-aged experimental stands as compared to seed crop in even-aged spruce stand (seed-crop observation stand Siilinjärvi 544, Hokkanen 2001) in 1990–2001. Standard deviations are marked as a segment on the bars.

conditions (Hokkanen 2000). The annual fluctuation of spruce seed crop in these uneven-aged monitoring plots was very similar to that in an even-aged seed-crop observation stand in the same geographical area (Hokkanen 2001, Fig. 5). This is logical because the main variables behind annual fluctuation of seed crop, climate and weather, are the same in uneven-aged and even-aged stands on the same site.

According to the results of this study, the amount of seed produced in an uneven-aged spruce-dominated stand was about one half that of an even-aged spruce stand. The obvious reason for this difference was the number of mature trees in the stand. In an uneven-aged stand the number of 'mature' trees ($d_{1.3}$ > 25 cm) is about 200 stems ha^{-1} (Lähde et al. 2002). On the monitoring plots the mean number of mature trees varied from 130 to 320 stems ha^{-1}. In a mature, low-thinned, even-aged spruce stand the corresponding figure is about 300–500 stems ha^{-1} (Vuokila and Väliaho 1980). When the density of mature spruce stems increased from 200 to 500 stems ha^{-1}, this meant that the seed production capacity increased threefold (Koski and Tallqvist 1978). This also largely explains the difference observed in the seed production capacity between the subplots with different stand basal area on the monitoring plots studied. These differences might have come more evident if the subplots in the same row would have had border zones also between each other (see Fig. 2).

On the other hand, mature trees in an uneven-aged stand may have a better position among neighbouring trees than do these in an even-aged stand. In an uneven-aged stand a mature tree of the same size may have a larger and more freely growing crown than in an even-aged stand. Larger crown often means better seed-production capacity per tree (Koski and Tallqvist 1978).

In southern Finland good cone years for spruce occur 3–4 times in ten years. In 1990 the spruce seed crop was the largest ever recorded in Finland (Hokkanen 2000). As a consequence of this excellent seed crop, in most monitoring plots in the beginning of the monitoring period the number of 'labile' seedlings (height < 11 cm) was high (see also Valkonen 1996). Towards the end of the monitoring period, part of these seedlings had moved to the upper height class ('stabilised' seedlings, (height > 10 cm)). Evidently, during the monitoring time the seedlings that had emerged from seed crops in 1993, 1996 and in 1999 were still mainly in category of 'labile' seedlings. There were no age determinations or individual follow-up of spruce seedlings in this study, but results of slow early development of spruce seedlings in an uneven-aged stand in other studies (e.g. Lundqvist 1989) support the above-mentioned development.

The emergence of germinants was strongly correlated with the seed crop of the same year, but even in a good seed year the variation between monitoring plots was large. This variation was due mainly to the weather conditions in the first summer (Yli-Vakkuri 1961, Valkonen 1996, de Chantal 2003). There was no correlation between stand characteristics and number of observed germinants. This is in accordance with the results of Lähde (1992) and Valkonen (1996).

Good seed crops create the basis for new, more or less visible cohorts in seedling height distribution and also for distribution of stem diameter. The mean number of 'stabilised' spruce seedlings was rather stable on one monitoring plot over the monitoring time. However, there was large variation within that monitoring plot and between experimental stands. Within the monitoring plot, about one third of the area was without spruce seedlings. The most southern field experiments were more fertile than the other experimental fields, which partly explains the lowest seedling densities. This kind of clustered spacing and large variation in density of spruce seedlings within and between stands is also familiar from earlier studies (Lundqvist 1989, Leinonen et al. 1989, Lähde 1992, Valkonen 1996).

Neither stand basal area nor stand volume had an influence on the number of 'stabilised' spruce seedlings (height over 10 cm), but these seedlings were taller on subplots with lower stand volume and lower basal area. This indicates that the competition from the overstorey trees plays a greater role as the seedlings grow taller. This observation is in an accordance with results reported by Lundqvist and Fridman (1996), Nilson and Lundqvist (2001) and Nilson (2001), which are mainly from Northern Sweden.

Ingrowth, i.e. the transition of seedlings to the sapling stage, also varied considerably from one monitoring plot to another. The monitoring period (5–10 years) in this study was too short to obtain reliable figures of the ingrowth in the long run. However, the adjusted mean of ingrowth, 26 stems ha^{-1} $year^{-1}$, was smaller than that for ingrowth measured (or calculated) on permanent plots managed with single tree selection in Sweden (Lundqvist 1989, 1991), but it was on the same level as observed on permanent plots managed with single tree selection in Finland (Lähde et al. 2002). On what level should regeneration be in order to fulfil the requirements of sustainable uneven-aged forest management? This question cannot be answered on the basis of the present results. In Sweden, however, some researchers have estimated that about 25 to 40 established seedlings per hectare and year should be enough for sustainable development in a boreal uneven-aged stand (Jeansson et al. 1989).

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