

## Seedling Establishment after Prescribed Burning of a Clear-Cut and a Partially Cut Mesic Boreal Forest in Southern Finland

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The prescribed burning of a 7.3 ha clear-cut and a 1.7 ha partially cut forest (volume 150 m<sup>3</sup>/ha) was carried out in Evo (61°12'N, 25°07'E) on 1 June 1992. The forest was a mesic *Myrtillus* site type forest dominated by Norway spruce (*Picea abies* (L.) Karst.). Practically all the trees and the above-ground parts of the understorey vegetation died in the fire, while the mor layer was thinned by an average of 1.5 cm.

A study was made on the change of germinated seedling populations in time and their dependence on environmental factors. Seedlings of Norway spruce, Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), pubescent birch (*B. pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L.) were inventoried in 1993 and in 1994 on permanent plots, four times per growing season. Autoregression models were used to compare regeneration of tree species in the burned forest with regeneration in the burnt clear-cut area, and to study the effect of distance from nearest seed source to regeneration.

The average number of seedlings germinating in 1993 was higher than in 1994, probably because of differences between these consecutive years in regard to the amount of seed rain and weather conditions. The number of Norway spruce and rowan seedlings was higher inside the forest area than in the clear-cut area. The distance to the bordering forest and to the closest seed trees did not explain the result. It is suggested that the more stable microclimatic conditions under the shade of dead trees promote germination and seedling establishment in the forest area. As rowan is a bird-dispersed species, it is likely that dead trees help the dispersal of rowan seeds by providing birds places to sit and defecate. The shade provided by dead trees may influence the further succession of the tree stand and vegetation composition and diversity.

**Keywords** prescribed burning, mesic forest, seed dispersal, seed rain, seedling establishment, autoregression models, GLM, *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Betula pubescens*, *Sorbus aucuparia*.

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## 1 Introduction

Fire is a natural factor in the boreal forest ecosystem. It maintains the diversity and the long-term stability of the forests. Most Fennoscandian, naturally developed coniferous forests have regenerated through secondary succession after forest fires, and fire has largely determined the structure of the boreal forest (e.g. Zackrisson 1977, Haapanen and Siitonen 1978, Engelmark 1987, Bradshaw 1993).

The generative regeneration of a burned area depends on seed availability. Tree species do not usually form soil seed banks (Harper 1977) and seeds on the humus surface are easily destroyed by fire. Usually tree populations develop after a fire from the seeds dispersed by the surviving trees and the bordering forests. The main factors influencing seedling establishment are: climatic and microhabitat conditions (prevailing wind conditions, light, precipitation, temperature, substrate), topography and seed and seedling predators.

The use of prescribed burning as a regeneration method in forestry diminished after the late 1960s, while scarification became more popular because of lower costs. The long period of efficient fire control and lack of appreciation of prescribed burning as a method to regenerate the forests resulted in little research on seedling establishment and post-fire forest regeneration. In recent years, prescribed burning has become more popular as a method for regenerating forest stands. Its usefulness in maintaining biodiversity on every organization level, from genetic to landscape level, has been widely accepted. It changes the nutrient, temperature and humidity conditions of the soil (e.g. Ahlgren and Ahlgren 1960, Viro 1969, Raison 1979) and promotes the natural regeneration of e.g. Scots pine (e.g. Lehto 1956) as well as the further development of young pine stands (e.g.

Yli-Vakkuri 1961b, Herr et al. 1994). It also decreases the propagation of pathogenic fungi and improves the natural tree stand development and succession of the whole forest ecosystem.

For economic reasons forest areas are normally clear-cut before burning. Since the temperature, light conditions and hydrology differ between spruce-dominated forests and open stands (e.g. Kuusisto 1984, Ross et al. 1986), it is likely that differences will also remain after the fire. It has been suggested that dead trees still provide shelter after fire (e.g. Engelmark 1993). This may also influence seedling establishment and further tree stand development. Prescribed burning has been recommended as a method to regenerate naturally protected and commercial boreal forests. The role and importance of the burned wood material to the tree stand development is, however, largely unknown.

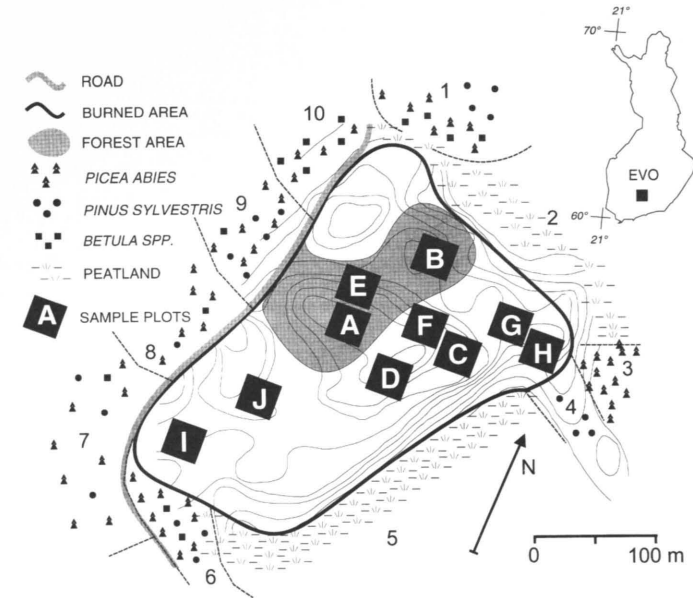
Our aims are:

1. To study the change in seedling populations after prescribed burning
2. To test if seedling establishment and survival in the early succession after prescribed burning is different in partially cut and clear-cut areas.
3. To find out if the distance from the bordering forest and the closest seed source has an effect on the seedling establishment in our data

## 2 Material and Methods

### 2.1 Study Area

The study area was in Evo in the Lammi municipality (61°12'N, 25°07'E) in southern Finland. The Evo area is situated in the southern boreal coniferous forest zone (Ahti et al. 1968). The study area represents mesic coniferous forest of



**Fig. 1.** The research area at Evo. For information of the bordering forests (1–10), see Table 1.

*Myrtillus* site type (*sensu* Cajander 1949), dominated by Norway spruce (*Picea abies* (L.) Karst.) before the burning.

The average of the yearly effective temperature sum (threshold temperature +5 °C) for the period 1951–1980 in the study area was 1115 d.d. (Elomaa 1988). Weather conditions differed considerably between 1993 and 1994. The effective temperature sum in the study area in 1993 was 1040, while in 1994 it was 1160. The average daily temperatures e.g. in July were markedly higher in 1994 compared with those in 1993. The average annual precipitation lies between 550–650 mm. The amount of precipitation in the study area was 108.8 mm in July 1993 while in July 1994 it was 6.3 mm. The number of rainy days were 21 and 4, respectively. The climatic data were provided by the Lammi biological station.

The bedrock below the research area is granite and quartz covered by morainic deposits. The dominating deposit type is fine moraine till.

### 2.2 Description of the Tree Stand

The average age of the tree stand, measured from 92 trees, was 115 years and the volume 280 m<sup>3</sup>/ha. The mean age of the Norway spruce was 93 years, with a wide age class distribution. Scots pine was more clearly represented by only one age class with a mean age of 160 years. The age of the birches was 90–100 years. Besides these dominating tree species, occasional stems of white alder (*Alnus incana* (L.) Moench), European aspen (*Populus tremula* L.) and willow (*Salix caprea* L.) occurred. These were generally less than 45 years old.

In 1992, prior to prescribed burning, an area of 7.3 ha in size was clearcut. A 1.7 ha forest area with a volume of 150 m<sup>3</sup>/ha was left in the centre (Fig. 1). Over 100 m<sup>3</sup>/ha was removed from this central area. This was mainly done by cutting Scots pine trees, together with some of the largest birches and Norway spruces. After the felling

**Table 1.** Description of the bordering forests (1–10) of the research area at Evo in Fig. 1.

	1	2	3	4	5	6	7	8	9	10
Age of the forest	45	5	65	125	5	135	145	125	95	45
Pine/spruce/birch, 1/10	0/5/5	0/0/10	0/10/0	10/0/0	0/0/10	3/6/1	3/6/1	1/8/1	7/2/1	0/1/9
Volume, m <sup>3</sup> /ha	34.0	0.0	264.0	40.0	0.0	263.0	425.0	96.0	62.0	195.0
Basal area, m <sup>2</sup> /ha	8.0	0.0	25.0	4.0	0.0	23.0	30.0	11.0	10.0	26.0
Dominant height, m	8.0	1.0	22.0	22.0	1.0	25.0	31.5	18.0	12.0	16.0

**Table 2.** General description of the sample plots (A–J) two years after the fire in 1994 and their distance from nearest seed trees. Forest sample plots A, B and E bold-faced.

	A	B	C	D	E	F	G	H	I	J
Distance to <i>Pinus sylvestris</i> , m	78	153	116	161	88	119	55	37	38	90
Distance to <i>Picea abies</i> , m	94	115	138	83	76	138	61	34	50	79
Distance to <i>Betula pendula</i> , m	95	150	133	173	75	142	65	38	53	73
Distance to <i>Betula pubescens</i> , m	95	142	190	230	86	168	78	89	60	80
Humus layer thickness, cm	4.3	4.8	5.1	4.7	5.6	3.6	2.7	4.2	4.7	5.2
Humus layer, SD	1.8	2.9	2.6	2.6	2.6	2.5	2.0	2.7	2.4	2.6
Stones, %-cover	4.4	6.9	7.7	6.2	6.3	17.7	13.5	9.9	11.8	10.8
Tree material, %-cover	5.7	3.0	3.7	4.7	4.0	3.3	2.0	4.3	3.3	4.2
Litter, %-cover	35.4	59.8	15.6	13.7	35.3	33.1	17.4	12.7	21.6	18.1

altogether 280 stems/ha were left (D1.3 > 100 mm), of which Norway spruce 232 stems/ha, Scots pine 37 stems/ha, pubescent birch 8 stems/ha, European aspen 1 stem/ha and white alder 2 stems/ha. The basal area/ha was 5.4 m<sup>2</sup> for Scots pine, 11.8 m<sup>2</sup> for Norway spruce, 0.3 m<sup>2</sup> for pubescent birch, and 0.1 m<sup>2</sup> for European aspen and white alder.

The saplings, 0.1–1.3 m in height, were inventoried in the whole research area before the prescribed burning in June 1992, using circular sample plots, 10 m<sup>2</sup> in size, placed as a grid throughout the area. The distance between two sample plots was 25 metres. The saplings were counted in altogether 116 sample plots. According to the inventory, 5129 saplings of Norway spruce, 1552 saplings of rowan, 302 saplings of birches, 112 saplings of common juniper (*Juniperus communis* L.), 95 saplings of white alder, 52 saplings of European aspen and 25 saplings of Scots pine were found per hectare. In the inventory of seedlings less than 0.1 m in height, the same grid and

circular sample plot of 1 m<sup>2</sup> in size was used. Only spruce seedlings were discovered: 36 000 individuals/ha.

The study area was bordered by open peatland from three directions; the western side was covered with a spruce-dominated old forest. Remnants of a spruce forest were also found on the eastern side of the research area (Fig. 1, Table 1). Some seed trees of Scots pine were left in the open area, but they died in the fire. The average distance from the sample plots to the bordering forests and to the nearest seed trees was 100 metres (Fig. 1, Table 2).

The prescribed burning was carried out on the 1st of June 1992. As a result of the rather dry logging waste, moderate wind speeds (3–6 m/s), hilly topography, the relatively large amount of understorey and the surrounding burning technique used, nearly all the trees were killed in the fire or shortly after. All the deciduous trees died in the fire. The conifers surviving the fire died later owing to the loss of needle biomass. In

1993 only 12 coniferous trees were alive and in 1994 only one. The surviving trees did not, however, contain any cones.

### 2.3 Field Methods

Ten permanent sample plots (30 × 30 metres in size) were established for the study of the burned research area. Three of these were located in the forest area (the average tree stand volume 150 m<sup>3</sup>), and three parallel plots in similar environments according to the topography and stoniness in the clear-cut area. In addition, 4 sample plots at different distances from the bordering stands were established in the clear-cut area (Fig. 1, Table 2). Thirty permanent circular plots were placed randomly on every sample plot. The size of each circle was 2 m<sup>2</sup> in this study. The inventory of the seedlings was done 4 times per growing season (in the beginning of June, July, August and September) in 1993 and 1994. The germination year of the seedlings of every tree species was determined. Only the data of seed-germinated seedlings was used in this study.

The stoniness of the sample plots A, B, C, D, E and F was measured using Viro's (1952) rod testing method. The coverage of stones, litter and tree material was estimated yearly on all sample plots during the vegetation inventories on every circle. The distance from the bordering stand (nearest seed trees) and thickness of the mor layer was measured for every sample plot (Table 2). The thickness of the mor layer prior to burning was measured at 16 systematically laid points in the forest area. During the inventory in 1994 the thickness of the mor layer was measured at 50–80 points on every sample plot.

### 2.4 Statistical Modelling

The change of seedling populations over a period of time and the dependence of the change on environmental factors were the main interest in this study. The differences between the forest and the clear-cut area, and the influence of the distance from the nearest seed trees on the development of each seedling cohort of the five tree species were tested by means of autoregression

models (Lindsey 1993). These were fitted as generalized linear models, GLM (McCullagh and Nelder 1989) using GLIM 3.77 (Payne 1986). An autoregression means introducing lagged responses as independent variables into the model (Lindsey 1993). This estimates the dependence of the current situation on the previous situations. The slope is determined by the rate of change in relation to the previous measurement. We tested the first order autoregression, i.e. the dependence of the cohort size on that of the immediately preceding measurement. We assumed that there were no seedlings before the first measurement, so it could be included in the data with zero values in the lagged variable.

We first fitted the lag variable 'lag', which was calculated as a logarithm of the lagged count plus one, into the model to estimate the common dependence on the preceding cohort size. This variable remained in the model regardless of its significance. If there was data from two years (the cohort born in 1993), the two-level factor 'year' was fitted after that. This variable was also left in the model, because it was sensible to assume that the autocorrelation is different in different years: birth and death processes operate during the first year, but only death will operate during the second. Finally, the two-level factor forest area–clear-cut area 'fore' and the distance from the nearest seed trees 'dist' were fitted into the model. When the significant main effects were in the model, pairwise interactions of the variables were tested; 'lag.year' first, followed by others. Fitting of 'dist', 'fore' and interactions was done in a stepwise manner.

The data were counts of seedlings per large sample plot, which in principal means that errors are Poisson distributed. However, the data were repeated measurements from permanent sample plots. In practice, this means that the data are clustered, and the first degree autoregression cannot completely explain the clustering. So, the data were overdispersed. However, this can be overcome by scaling the deviance of the model by its degrees of freedom (McCullagh and Nelder 1989). We used Poisson error with logarithm link and performed the overdispersion scaling by using an F-test instead of the chi-square test (Aitkin et al. 1989, McCullagh and Nelder 1989).

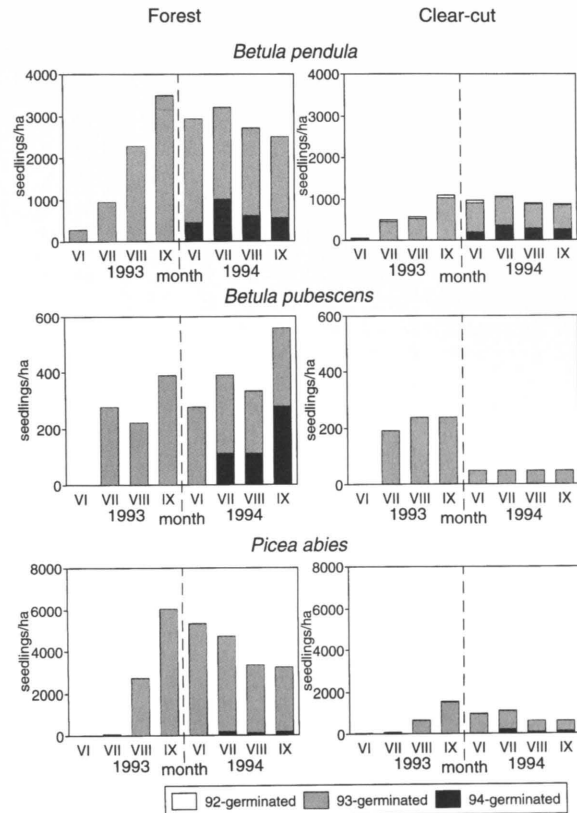


Fig. 2. Seedling establishment after prescribed burning in Evo. The number of *Betula pendula*, *Betula pubescens* and *Picea abies* seedlings of different age discovered in every inventory in the forest and the clear-cut area.

## 3 Results

### 3.1 General Development of the Stand

Of the six sample plots, E and F were very stony, belonging to stoniness class III according to Viro (1952). The other four sample plots (A, B, C and D) belonged to stoniness class II. The coverage of stones was largest on sample plot F. On an average, the sample plots in the forest area were somewhat less stony than those in the clear-cut area.

The percentage cover of tree material was small on every sample plot. The percentage cover of litter was still high in the forest area two years after the fire, because of the large amount of needle rain (Table 2). The mor layer thickness prior to the prescribed burning varied from 4.5 to 8.5 cm, the average being 6.4 cm. After the fire the average mor layer thickness was 4.9 cm in the forest area and 4.3 cm in the clear-cut area, the average in the whole study area being 4.6 cm. The sample plots in the clear-cut area were somewhat

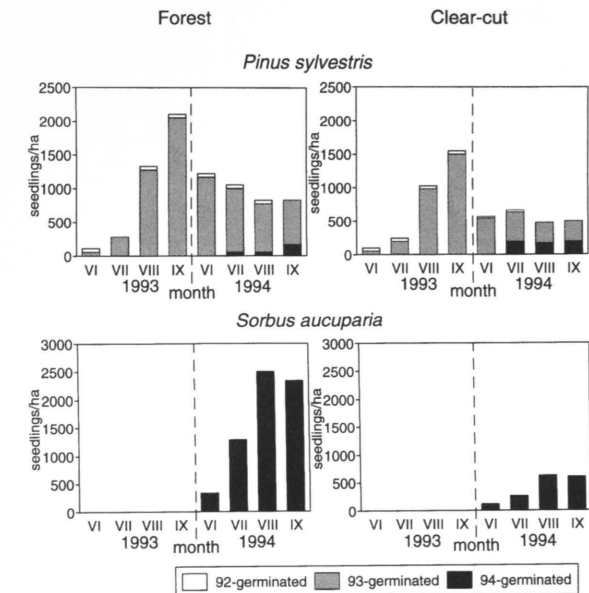


Fig. 3. Seedling establishment after prescribed burning in Evo. The number of *Pinus sylvestris* and *Sorbus aucuparia* seedlings of different age discovered in every inventory in the forest and the clear-cut area.

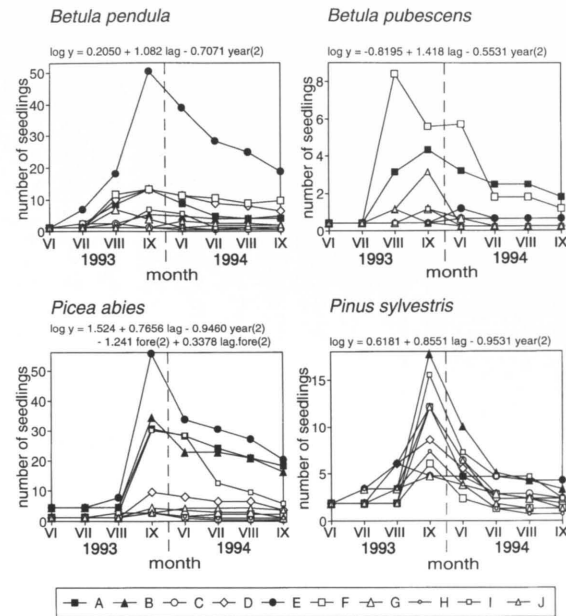
closer to the seed trees than the sample plots in the forest area, but variation between the sample plots was large (Table 2). The distance to the nearest rowan was not measured, but there were none in the tree layer near the study area.

Species that regenerated vegetatively from underground parts were rowan, European aspen and both the pubescent and the silver birch. Tree species that germinated from seeds were Norway spruce, Scots pine, both birches and rowan.

In September 1993, the average number of seedlings in the whole study area was 1717 per hectare for Scots pine, 2900 for Norway spruce, 1817 for silver birch, 283 for pubescent birch and none for rowan. Only a minority of the seedlings germinated in 1992. In September 1994 the comparative results were 617 for Scots pine, 1383 for Norway spruce, 1300 for silver birch, 217 for pubescent birch and 933 for rowan. The majority of these seedlings germinated in 1993 (Figs. 2 and 3).

At the end of both inventory years the number of seedlings of all tree species was higher in the forest area than in the clear-cut area (Figs. 2 and 3). For silver birch this was merely due to the high number of seedlings in sample plot E. Some silver birch seedlings germinating in 1992 were detected in the clear-cut area, but none in the forest area. The number of silver birch seedlings was generally higher than that of the pubescent birch (Fig. 2).

There were more Norway spruce seedlings in the forest area than in the clear-cut area. In September 1993, 6055 seedlings per hectare were detected in the forest area. The corresponding amount in the clear-cut area was 1523 seedlings per hectare. One year later, 3056 seedlings per hectare in the forest area and 905 seedlings per hectare in the clear-cut area were still alive (Fig. 2). In September 1993, the number of Scots pine seedlings which had germinated during the same



**Fig. 4.** Fitted values of autoregression models for seedlings germinating in 1993. The model is shown under the name of each species. The sample plots A, B and E were located in the forest area, the rest of the sample plots in the clear-cut area.

year was 2055 per hectare in the forest area. In the clear-cut area the corresponding amount was 1500 seedlings per hectare. One year later 667 seedlings per hectare were still alive in the forest area. In the clear-cut area 429 seedlings per hectare were counted. The number of coniferous tree seedlings which had germinated in 1994 was markedly lower than in 1993 (Figs. 2 and 3).

In 1993 we found no establishment of rowan seedlings. In 1994 the number of rowan seedlings was larger inside the forest area (2333 seedlings per hectare) than in the clear-cut area (333 seedlings per hectare) (Fig. 3).

### 3.2 Autoregression Models

Autocorrelation in time was strong for seedlings of all tree species germinating in 1993. This

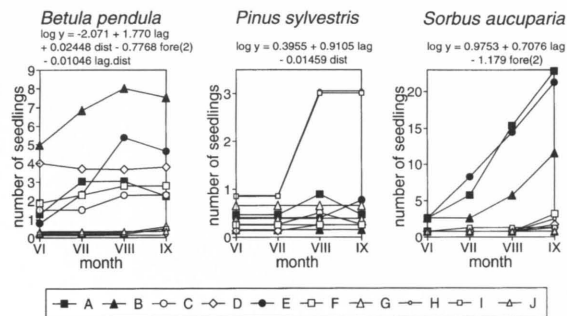
means that there was not much random variation in the change of the cohort size. In general, the change in the number of seedlings was rather stable during the growing season for every tree species after the fire (Fig. 4). But, of course, the trend was on the upswing in 1993 and on the downswing in 1994.

For all species, the parameter estimate for the second year ('year(2)') was negative. This means that in 1994 the number of seedlings was smaller than in 1993 in relation to the preceding measurement. This is natural since during the first year of studying the 1993 cohort (Table 3, Fig. 4), both establishment and mortality operate while during the second year only mortality operates.

The distance to the nearest seed trees did not have a significant effect on the population size of silver birch, pubescent birch or Scots pine. Neither did the two-level factor forest area–clear-

**Table 3.** Analysis of deviance tables, F-ratios and P-values of autoregression models for seedlings of different species germinating in 1993. See text for modelling details.

	Deviance	$\Delta$ Dev	df <sup>err</sup>	$\Delta$ df <sup>err</sup>	F	P
<i>Betula pendula</i>						
null	723.5		79			
lag	172.2	551.3	78	1	249.70	0.000
lag+year	122.7	49.5	77	1	31.07	0.000
lag+year+dist	120.7	2.0	76	1	1.36	0.264
lag+year+fore	120.2	2.5	76	1	1.59	0.211
lag+year+lag.year	122.3	0.4	76	1	0.25	0.620
<i>Betula pubescens</i>						
null	186.1		79			
lag	99.1	87.1	78	1	68.58	0.000
lag+year	93.3	5.7	77	1	4.73	0.033
lag+year+dist	93.3	0.0	76	1	0.02	0.899
lag+year+fore	90.4	2.9	76	1	2.44	0.123
lag+year+lag.year	90.7	2.7	76	1	2.23	0.139
<i>Picea abies</i>						
null	1067.8		79			
lag	356.9	710.9	78	1	155.40	0.000
lag+year	229.9	127.0	77	1	42.54	0.000
lag+year+dist	229.2	0.7	76	1	0.23	0.634
lag+year+fore	210.4	19.4	76	1	7.02	0.010
lag+year+fore+dist	206.9	3.6	75	1	1.29	0.260
lag+year+fore+lag.year	210.3	0.1	75	1	0.05	0.830
lag+year+fore+lag.fore	191.8	18.6	75	1	7.29	0.009
lag+year+fore+year.fore	209.2	1.2	75	1	0.44	0.507
lag+year+fore+lag.fore+lag.year	191.7	0.1	74	1	0.04	0.845
lag+year+fore+lag.fore+year.fore	190.2	1.7	74	1	0.64	0.426
<i>Pinus sylvestris</i>						
null	305.2		79			
lag	201.7	103.5	78	1	40.04	0.000
lag+year	140.1	61.6	77	1	33.86	0.000
lag+year+dist	139.5	0.6	76	1	0.32	0.572
lag+year+fore	135.9	4.2	76	1	2.36	0.129
lag+year+lag.year	139.9	0.1	76	1	0.07	0.784



**Fig. 5.** Fitted values of autoregression models for seedlings germinating in 1994. The model is shown under the name of each species. Notice that the Poisson error distribution did not fit sufficiently well for *Pinus sylvestris*.

cut area have an effect on the autocorrelation for these species. Variable 'fore' did, however, have a significant effect on the autocorrelation for Norway spruce. The interaction 'lag.fore' was also included in the model. The changes in cohort size were faster in the forest area than in the clear-cut area. Moreover, the number of seedlings was larger (Fig. 4).

In 1994 the establishment of seedlings was markedly lower, which made the interpretation of the modelling results more difficult. For Norway spruce, none of the variables was significant. So, it was not possible to build a satisfying model. By checking the data it was noticed that the seedling establishment of Norway spruce was rather random in 1994 and the seedlings died shortly after germination. The number of pubescent birch seedlings was even smaller, so it was also impossible to build a model for this species (see Fig. 2).

In data of other species, autocorrelation was strong in the cohort germinating in 1994. In the model of Scots pine the Poisson error did not fit reasonably well and therefore a firm interpretation can hardly be made (Table 4, Fig. 5).

The number of silver birch seedlings was higher in the forest area than in the clear-cut area when compared with the previous inventory. The distance to the seed trees was significant (Table 4), but did not have much influence because the

regression coefficient was small (Fig. 5). Since the interaction term 'lag.dist' could be included in the model, the autocorrelation was different at different distances. The average change was dependent on the distance to the bordering forest (Fig. 5).

In the model for rowan the two-level factor forest area–clear-cut area was significant (Table 4). The number of seedlings was larger inside the forest area than in the open area and the difference was quite clear (Fig. 5).

## 4 Discussion

The boreal tree species in Finland do not usually form a persistent seed bank. In general, birch seeds survive better than seeds of conifers (Yli-Vakkuri 1963), but are still short-lived. According to Granström (1985) the seeds of pubescent birch and silver birch may stay viable in a seed bank for a couple of years. Seeds of the boreal trees are mainly concentrated in the upper mor layer and are therefore consequently easily destroyed in the fire. Maximum temperatures on the ground have been measured at 779 °C during prescribed burnings (Vasander and Lindholm 1985) and in such temperatures the seeds are surely killed (e.g. Ahlgren and Ahlgren 1960). The mor

**Table 4.** Analysis of deviance tables, F-ratios and P-values of autoregression models for seedlings of different species germinating in 1994. See text for modelling details.

	Deviance	ΔDev	df <sup>err</sup>	Δdf <sup>err</sup>	F	P
<i>Betula pendula</i>						
null	112.9		39			
lag	64.8	48.1	38	1	28.24	0.000
lag+dist	55.9	8.9	37	1	5.92	0.020
lag+fore	58.1	6.7	37	1	4.28	0.046
lag+dist+fore	39.4	16.4	36	1	14.98	0.000
lag+dist+fore+lag.dist	31.7	7.8	35	1	8.59	0.006
lag+dist+fore+lag.fore	39.2	0.2	35	1	0.20	0.657
lag+dist+fore+dist.fore	33.3	6.1	35	1	6.45	0.016
lag+dist+fore+lag.dist+lag.fore	31.0	0.6	34	1	0.70	0.407
lag+dist+fore+lag.dist+dist.fore	30.0	1.6	34	1	1.91	0.176
<i>Picea abies</i>						
null	35.6		39			
lag	35.6	0.0	38	1	0.00	1.000
lag+dist	35.4	0.2	37	1	0.22	0.644
lag+fore	35.5	0.1	37	1	0.13	0.720
<i>Pinus sylvestris</i>						
null	63.0		39			
lag	43.5	19.5	38	1	16.98	0.000
lag+dist	37.6	6.0	37	1	5.88	0.020
lag+fore	43.3	0.2	37	1	0.18	0.677
lag+dist+fore	37.6	0.0	36	1	0.00	1.000
lag+dist+lag.dist	36.1	1.4	36	1	1.43	0.240
<i>Sorbus aucuparia</i>						
null	286.5		39			
lag	88.0	198.5	38	1	85.75	0.000
lag+fore	66.6	21.4	37	1	11.87	0.001
lag+fore+lag.fore	64.7	1.9	36	1	1.06	0.311



layer thickness results indicate that the mor consumption was rather similar in the compared areas. Since the trees were also killed in the fire it is very likely that the seeds in the study area were totally destroyed in the fire. All the seed material must have come to the area after the fire, and the seedling establishment was dependent on seed dispersal from the bordering forests.

The seeding distance for birch species is generally long, but they differ to some extent according to the seeding capacity (e.g. Sarvas 1948). It is likely that there was rather high dispersal of birch seeds in the research area even though the average distance from the seeding birches was over 100 metres (Table 2). According to Sarvas (1948) the seeds of pubescent birch fall more quickly than seeds of silver birch. Therefore silver birch has an advantage in conquering higher sites and sites farther away from the bordering forests. This may partly explain why our data shows a higher number of silver birch seedlings than pubescent birch seedlings. Norway spruce seeds can disperse as far as 200 metres from the seed tree and on snow cover even farther. In addition, the number of empty seeds increases with increasing distance (Heikinheimo 1932). The distance from the sample plots to the nearest seeding spruce varies, but on an average it is longer for the sample plots in the forest area than for those in the clear-cut area (Table 2). The maximum seeding distance for Scots pine seeds is 70–100 metres, being most effective under a distance of 30–40 metres (Lehto 1956). The sample plots were far away from the effective seed shadow of pine, and regeneration was therefore partly restricted by the availability of seeds. The Scots pine seed trees left in the research area may, however, have had a small effect on seedling establishment in 1993, but this is unlikely since they were practically all killed in the fire.

Birds, e.g. thrushes (*Turdus* sp.) and waxwings (*Bombicilla garrulus*) are important dispersers of rowan seeds (Pokorný 1973, Mitchell 1986). Since there were no rowans in the tree layer in our research area or in its close vicinity, it is likely that the rowan seeds were carried to the research area by birds.

The majority of spruce seeds fall in April–May (Heikinheimo 1932) and therefore practically no Norway spruce seedlings were established in

summer 1992. Scots pine seeds drop mainly in May–June (Heikinheimo 1932) and some pine seedlings originating from summer 1992 were also found in our material. Most of the birch seeds fall in August–September and germinate the following summer (Heikinheimo 1932). This is reflected in our material; there were no seedlings of pubescent birch and only very few seedlings of silver birch germinating in 1992.

The annual seed rain varies markedly. In 1993 the seed rain for every tree species studied in the Evo district was higher than in 1994, e.g. the number of ripening cones of coniferous trees decreased significantly in seed rain study forests in southern Finland from 1992 to 1994. The seed production of birches in 1993 was the highest observed during the last 20 years. In 1994 seed production was markedly low (unpublished material by Tatu Hokkanen, The Finnish Forest Research Institute). The fact that the number of seedlings germinating in 1993 was larger than in 1994 is therefore probably caused by the climatic conditions, which were better for germination in 1993 than in 1994. During the growing season the precipitation was higher in 1993 compared with 1994 and the temperatures during the extremely warm summer of 1994 were probably too high for germination of most of the tree species studied, at least in the clear-cut area. The data also suggests that at least some part of the birch seeds falling in 1993 also germinated in the same year.

Prescribed burning has been known to change the properties of the soil for decades (e.g. Ahlgren and Ahlgren 1960, Viro 1969, Raison 1979). After fire, for instance, the water retention property changes, since it depends on the amount of organic matter on the surface. This influences seedling regeneration and survival (e.g. Mallik et al. 1988). According to Yli-Vakkuri (1961a), seedling establishment after prescribed burning is low during the first years, but the conditions for regeneration become better 3–5 years after a fire (see also Sarvas 1937, Engelmark 1993, Schimmel 1993).

During the growing season, the daily averages of air and soil temperatures, wind velocity, and short-wave radiation are consistently lower, and soil and air moisture are higher inside the forest than in the clearcut area. Further, the daily fluctuation of all these variables is lower in the for-

est than in the open area (Chen et al. 1993). The proximity of living seed trees has been found to have a negative effect on the growth of seedlings and also on other vegetation (Kuuluvainen and Pukkala 1989). Dead trees have a different effect, since there is no nutrient and water uptake. Dead trees provide shade after a forest fire and Norway spruce has been found to establish before Scots pine in the shade of dead trees in mesic sites after a fire (Engelmark 1993). Dead trees also change the microclimatic conditions and after falling down they provide nutrients and substrate for germination and seedling establishment. In our study, seedlings of both coniferous trees were found in the partially cut forest, but their further development is still unknown.

The optimal germination temperature for Norway spruce is +21 °C, and germination rapidly decreases as temperatures exceed +23 °C (Leinonen et al. 1993). In clear-cut areas the surface temperature of humus can rise above +30 °C (Viro 1974). In the burned clear-cut area the temperatures can be even higher, because of the lack of vegetation cover and, moreover, as a result of increased light absorption by the blackened surface and by the presence of charcoal in the soils (Ahlgren and Ahlgren 1960). The conditions for Norway spruce seed germination are therefore better inside the burned forest area, where maximum and minimum temperatures are likely to be less extreme and evaporation lower than on the open area.

The two years under study differed from each other in the amount of seed rain, temperature, insolation and precipitation. The dry seasons together with the often common extreme temperature conditions on black surfaces may be fatal to tree seedlings. The advantages of increased shelter should have been more pronounced during the drier year of 1994 than in 1993. However, seedling establishment was not markedly better in the forest than in the clear-cut area. Since the number of seedlings per plot was generally low in 1994, this could be a sampling error.

In the beginning of succession, the understorey vegetation can have a positive effect on seedling establishment because of the more stable micro-environment in the shelter of vegetation cover (Connell and Slatyer 1977). However, as a result of competition in the later succession, vegetation

has a harmful effect on both seedling establishment and survival (Hertz 1932, 1935, Lehto 1956). The mean total coverage of the understorey vegetation was 0.4 % in 1992, 15.1 % in 1993 and 40.1 % in 1994. No significant difference in vegetation cover was detected between the forest and the clear-cut area (Vanha-Majamaa et al. 1995). It is likely that the vegetation cover is not yet too dominating to hinder seedling establishment, and may offer more stable microclimatic conditions for seedling growth than a totally plain surface because it stabilizes radiation, moisture and temperature conditions on the ground. Seedling establishment is thereby also connected to the development of vegetation cover.

Since the seed rain in the research area was not studied, it is impossible to clarify the effects of factors such as wind conditions or topography on the seeding of different sites in the research area. It is clear that two years is too short a period for evidence on how seedling establishment will develop in the future. Further studies are needed to clarify the significance of different microsites, such as burned wood material, to seedling establishment and survival. This should be done especially on a scale of individual seedlings and their immediate surroundings in order to clarify microhabitat requirements. Without measurements of light, temperature and moisture conditions the interpretation of the results is also more difficult.

## 5 Conclusions

The results show a clear difference in seedling establishment during post-fire years. This is in accordance with the information on the differences in seed rain and weather conditions for the subsequent years. The number of seedlings was generally higher inside the forest area than in the clear-cut area. This was especially true for the seedlings of Norway spruce germinating in 1993. It is suggested that this can be explained by more stable microclimatic conditions inside the forest area than in the open area. It was shown that the distance from the bordering forest could not explain the difference.

The number of rowan seedlings in the 1994

data was higher inside the forest area than in the open area. Rowan is a bird-dispersed tree and it is therefore suggested that the forest area, by offering birds more places to sit and defecate, thereby help rowan to disperse. This may even cause changes in further tree stand development.

In general, young seedlings have a high mortality rate. In this study the mortality of the seedlings in the burned area, especially in the forest area, seems to be rather low when taking into account the rather extreme conditions in 1994. According to the results it seems possible that by leaving some tree material in burned areas it is possible to make natural regeneration easier, at least for Norway spruce seedlings. The amount of tree material needed is yet unknown. The results also point out clearly the importance of taking into account the yearly variation in seed rain in natural regeneration. By timing prescribed burning according to the abundant seed years of e.g. Scots pine, seedling establishment could be increased.

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