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Natural regeneration of *Picea abies* on small clear-cuts in SE Norway

Kjersti Holt Hanssen*

Department of Forest Sciences, Agricultural University of Norway, P.O. Box 5044, N-1432 Ås, Norway

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Abstract

The objective was to study the influence of vegetation cover, humus depth, microrelief and distance to seed tree edge on natural regeneration of Norway spruce (*Picea abies* (L.) Karst.) in five small clear-cuts on bilberry woodland in southeastern Norway. The impact of the vegetation was considered at tree different scales: at the growing point, in the nearest square decimetre around the seedlings and at a 1 m^2 scale. Most of the regeneration (95%) developed in 1996, after a rich seed year in 1995. The microhabitat was of crucial importance to seedling establishment. Litter, *Sphagnum* spp. and *Polytrichum commune* were good substrates for establishment, while areas dominated by *Deschampsia flexuosa*, *Dicranum* spp. and *Pleurozium schreberi* had very few seedlings. Seedling survival after five growing seasons was slightly better in litter than in *Sphagnum* and other mosses, but the differences were not statistically significant. Increasing humus depth had a positive influence on regeneration, probably due to shallow soils at the sites. Even though depressions covered only 4.9% of the ground, 24.1% of the seedlings occurred here. Survival was, however, lower in depressions than in the other microrelief classes. Distance to the seed tree edge had a significant influence on establishment, with more seedlings establishing close to the edge.

Keywords: Natural regeneration; Microhabitat; Microrelief; Seedbed; Norway spruce

1. Introduction

Norway spruce (*Picea abies* (L.) Karst.) is a species native to Norway, and spruce dominated forests cover 40% of the productive forest area and constitute 45% of the timber volume (Tomter, 1999). Since the 1950s, spruce forests in Norway have mostly been clear-cut, and regenerated by planting. The last years, however, there has been an increase in the use of natural regeneration to: (1) decrease the costs of regeneration; (2) apply a "close-to-nature" kind of forestry, in which the use of smaller clear-cuts and naturally provided seeds are parts; and (3) increase plant density, get denser stands and hence improve the timber quality. Natural regeneration is especially interesting in areas with low to medium productivity, as lower profitability in these areas allows only small investments.

At present, the most frequently used method for natural regeneration of spruce in Norway is to make small clear-cuts, and then leave the area to natural seeding from stands nearby. Often, the ground is not scarified. The regeneration success using this method can be highly variable. Controls of natural regeneration in conifer stands 2 years after logging showed that at least 41% of the stands needed scarification or supplementary planting to obtain satisfactory regeneration densities (NIJOS, 2001). Consequently, there

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* Tel.: +47-64-94-88-91; fax: +47-64-94-88-90.
E-mail address: kjersti.hanssen@isf.nlh.no (K.H. Hanssen).

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is a demand for more knowledge about the factors that affect natural regeneration of spruce on clear-cuts.

Failure of natural regeneration may be caused by lack of mature seeds, or lack of 'safe sites' (Harper, 1977) for germination and seedling survival. Summer temperatures will influence flowering intensity (Brøndbo, 1970; Ilstedt and Eriksson, 1982) and seed ripening (Opsahl, 1952). The frequency of seed years will therefore vary with altitude and degree of latitude (Sarvas, 1957). Spruce has a large between-year variation in seed production (Skoklefald, 1966; Koski and Tallqvist, 1978), and few seed years for spruce, especially at higher altitudes, is clearly a limiting factor for regeneration (Mork, 1968; Skoklefald, 1985). The spruce seeds will usually disperse within a limited distance from the mother tree, and distance to seed trees will therefore be of importance to numbers and quality of seeds on a particular spot (Hesselman, 1938).

In seed years, the number of seeds that reach the ground can be up to several hundreds per square meter (Sarvas, 1957; Skoklefald, 1966; Koski and Tallqvist, 1978). Still, only a fraction will germinate and produce seedlings. The microhabitat for a seed or seedling will consist of its immediate surroundings, with vegetation, humus layer and microrelief as major components. As both abiotic and biotic factors can differ between microhabitats, their role for seedling emergence and establishment has been emphasised in recent years (Ohlson and Zackrisson, 1992; Oswald and Neuenschwander, 1993; St. Hilaire and Leopold, 1995; Hörnberg et al., 1997).

The distribution and composition of the vegetation community may determine whether there are seedlings present or not (Siren, 1955; Kuuluvainen, 1994). Bottom- and field layer species in the vicinity of seedlings compete for water, light and nutrients (Örlander et al., 1996; Hörnberg et al., 1997; Jäderlund et al., 1997; Cornett et al., 1998) and sometimes inhibit seed germination and seedling growth by allelopathy (Nilsson and Zackrisson, 1992; Pellisier, 1993; Dolling et al., 1994; Gallet, 1994; Jäderlund et al., 1998). Seed and seedling predation may also vary with seedbed substrate (Lekander and Söderström, 1969; Nystrand and Granström, 1997; Örlander and Nilsson, 1999). Quite a few studies have documented the positive effect of scarification on regeneration of conifers, as removal of the vegetation and humus layer secures a more stable water supply (Yli-Vakkuri, 1963; Örlander et al., 1998; Béland et al., 2000; Oleskog and Sahlén, 2000) as well as reducing negative effects of some of the factors mentioned above. As a substantial number of the clear-cuts left to natural regeneration are not scarified, it is important to study regeneration in intact vegetation in detail.

Several authors have found microrelief to be important for emergence and establishment of tree seedlings on unscarified ground, for instance on peatlands (St. Hilaire and Leopold, 1995; Hörnberg et al., 1997; Gunnarsson and Rydin, 1998; Roy et al., 1999), on burnt sites (Filion and Morin, 1996; Kuuluvainen and Rouvinen, 2000) and in high-altitude old-growth stands (Hytteborn et al., 1987; Hofgaard, 1993; Szewczyk and Szwagrzyk, 1996). The influence of microrelief on clear-cuts on mineral soil is less studied.

This study is a part of the project "Alternative forest management", where biological, technical and economical consequences of alternative forestry practices are investigated. Alternative practices studied include shelterwood felling, reduced size of clear-cuts and the use of natural regeneration (Andreassen, 1998). In this paper, natural regeneration on small clear-cuts will be addressed. The objective was to study the influence of vegetation, thickness of humus layer and microrelief on seedling establishment and survival, and if distance to seed source affected the regeneration pattern.

2. Materials and methods

2.1. Study stands and treatment

The study was performed in the autumns of 1996–2000 on five 50 m × 50 m clear-cuts in southeastern Norway (Table 1). Three of the sites, Høgås I and II and Kolltjern, are located in the Ringkollen area, while Hof and Lindberget are situated in the Solør area further east (Fig. 1A). The altitudes vary from 470 to 620 m a.s.l., and site indices are low to medium (Tveite, 1977). They were harvested with single-grip harvesters and forwarders during the winters of 1993/1994 and 1994/1995. Stem density prior to logging varied from 736 to 1164 stems ha^{-1}, and all stands were multi-storied. The vegetation type for all five areas was bilberry (Eu-Piceetum myrtilletosum) woodland (Fremstad, 1997), which is the most common

Table 1
Stand characteristics of the studied clear-cuts at Ringkollen (1–3) and Solør (4–5)

Stand	Latitude and longitude	Altitude (m a.s.l.)	Stems ha^{-1} prior to logging	Volume prior to logging (m^3 ha^{-1})	Site ind. (H_{40})[a]	Exposure	Cut year
1. Høgås I	60°08′N and 10°26′E	590	1052	179	10.7	E	1994/1995
2. Høgås II	60°08′N and 10°26′E	570	736	126	11.0	S	1994/1995
3. Kolltjern	60°10′N and 10°24′E	620	1012	195	11.0	S	1994/1995
4. Hof	60°31′N and 11°45′E	470	1164	229	13.6	SW	1993/1994
5. Lindberget	60°49′N and 12°12′E	570	868	186	7.5	NW	1993/1994

[a] Defined as dominant height in meters at a reference age of 40 years in breast height (Tveite, 1977).

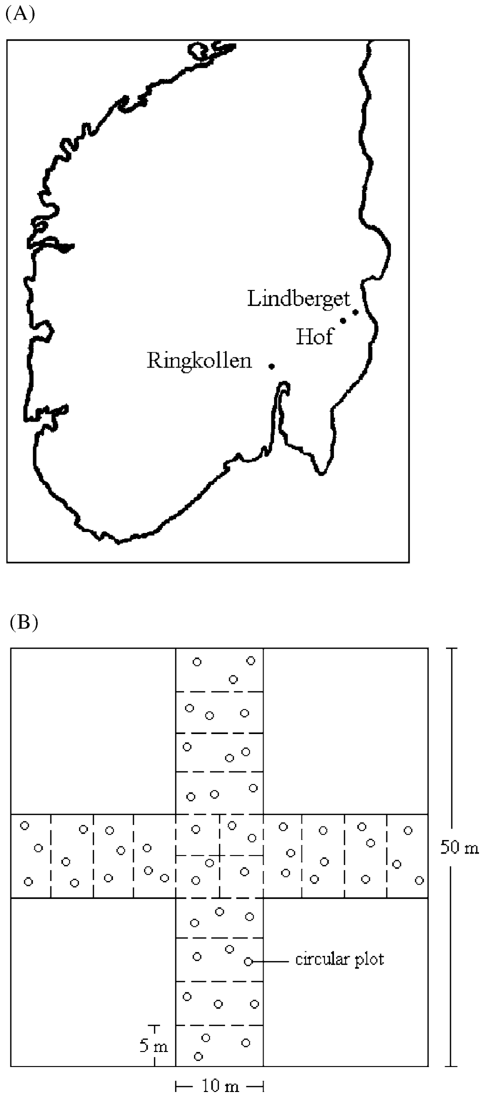

Fig. 1. (A) The location of the studied sites in SE Norway; Ringkollen (Høgås I and II, Kolltjern), Hof, and Lindberget. (B) The design of the study on each clear-cut.

forest vegetation type in Norway, covering 35% of the productive forest area (Larsson et al., 1994). The clear-cuts were dominated by wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.) and bilberry (*Vaccinium myrtillus* (L.)) in the field layer, while the bryophytes *Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp. (Hedw.) and *Hylocomium splendens* (Hedw.) Schimp. dominated the ground layer (Table 2). Some *Sphagnum* spp. (L.) were present at all sites. The soil types are humo ferric podsols derived from glacial till (Agriculture Canada Expert Committee on Soil Survey, 1987). As a part of other experiments, each clear-cut was spot-scarified with an excavator.

2.2. Climate

Total monthly precipitation and mean air temperature (°C) were obtained from the nearest meteorological stations (Fig. 2). Temperatures for the Ringkollen sites are from Gardermoen meteorological station (60°12′N, 11°04′E, 202 m a.s.l.), and precipitation from Lunner (60°17′N, 10°34′E, 372 m a.s.l.). The nearest station with temperature measurements for both Hof and Lindberget is Vinger (60°13′N, 12°01′E, 175 m a.s.l.), while for precipitation the nearest station is Rundberget (60°49′N, 12°06′E, 347 m a.s.l.). Temperatures were adjusted for the height difference between the meteorological station and the sites with -0.6 °C for each 100 m (Børset, 1985).

2.3. Seed years

The Norwegian Forest Seed Station collects data from the municipalities on seed setting every year, and they also test seed ripening in the various cohorts. The data in Table 3 is obtained from forestry adviser Tore Wetlesen (pers. comm.).

Table 2
Mean cover and frequency of species or substrates on circular plots ($n = 251$) in 1996, and t-test for change 1996–2000

Species	Mean cover (%) 1996	Frequency (%) 1996	Change in cover (%) 1996–2000	*P*	Correlations with microrelief classes[a]			
					Level ground	Sloping ground	Depressions	Elevations
D. flexuosa	40.6	90.4	16.4	0.0001	++	−−		−−
Dicranum spp.	20.1	78.1	−11.2	0.0001				
V. myrtillus	15.3	98.4	−2.1	0.05	−−	++		++
Litter	11.6	82.5	−3.3	0.01	−	+		
P. schreberi	7.5	57.0	−3.3	0.001				++
Branches	7.0	62.2	−4.3	0.0001				
S. girgensohnii	5.0	13.9	−1.7	0.01	+	−		
V. vitis-idaea	2.7	66.5	5.3	0.0001				
H. splendens	2.0	23.5	−0.2	n.s.				+
Calluna vulgaris	0.6	12.4	1.5	0.0001				
P. crista-castrensis	0.6	7.6	−0.2	n.s.				
Cladonia spp.	0.5	14.3	−0.1	n.s.				
Stumps and roots	0.5	12.7	0.2	0.001				
Barbilophozia lycopodioides	0.4	7.2	−0.3	n.s.				
P. commune	0.4	8.0	1.3	0.001				
Linnea borealis	0.3	17.9	1.8	0.0001				
Trientalis europaea	0.1	21.1	0.3	0.0001				
Luzula pilosa	0.1	7.2	0.2	0.0001				
Decidious spp.	0.1	13.1	0.2	0.0001				
Epilobium angustifolium	0.1	2.8	0.1	n.s.				
Rubus idaeus	0.1	4.4	1.1	0.0001				
Mineral soil	0.04	4.8	−0.03	0.01				
Melampyrum pratense	0.02	4.8	0.4	0.0001				
Maianthemum bifolium	0.02	7.2	0.1	0.0001				

[a] Significant correlations between cover of vegetation species and microrelief classes in the circular plots are shown by signs. +/−: correlations (positive/negative) are significant at the 0.05 level. ++/−−: correlations are significant at the 0.001 level. Species included in the table were present in at least 2% of the circular plots.

2.4. Natural regeneration, vegetation and microrelief

In the autumn of 1996, about 50 circular plots of size 1 m^2 were laid out across each of the five clear-cuts, from the middle of one side of the clear-cut to the other within a 10 m wide transect, and then between the remaining sides. Thus, circular plots were laid out in a cross-like pattern (Fig. 1B) to get an even number of

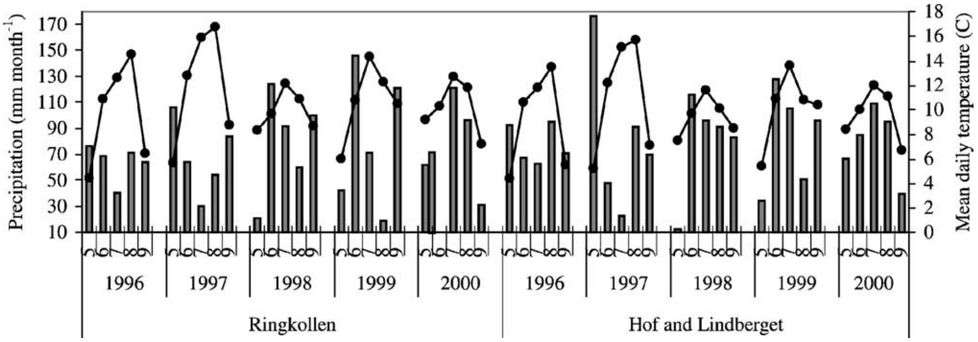

Fig. 2. Total monthly precipitation (bars) and mean daily air temperature (lines) from May to September for the locations in the study.

Table 3
Seed setting and ripening conditions for Norway spruce above 450 m in the Ringkollen and Solør areas 1993–2000 (data from the Norwegian Forest Seed Station)

Year	Seed setting[a]		Ripening conditions
	Ringkollen	Solør	
1993	1	1	
1994	0–1	1	
1995	3	3	Good
1996	1	1	
1997	1	0–1	
1998	2	2	Poor
1999	1	0	
2000	1	0	

[a] 0: no seed setting, 1: negligible, 2: good, 3: very good.

plots at different distances and at different exposures to the edges of the remaining stands. The circular plots were placed outside the scarified spots and other areas where the vegetation layer was disturbed, with three circular plots for each 5 m of the 10 m wide transect. Sometimes only two circular plots were laid out for each 5 m, due to lack of suitable undisturbed areas. The middle of each plot was marked with a stick. In each plot, the spruce seedlings, also dead ones, were counted. Seedlings older than one season were age determined by counting branch whorls. The vegetation cover of each circular plot was registered. Substrates such as litter, branches and stumps were included in the vegetation analysis. On each second plot, the thickness of the humus layer was measured. The following year, the seedlings were counted again, and marked with a 10 cm plastic stick. In a circular plot of 1 dm^2 around each seedling (from now on called seedling plots), the microrelief type (classified as level ground, sloping ground, depression or elevation) and vegetation cover were recorded, as was the vegetation at the very point where the seedling grew (henceforth called the growing point). Thus, the vegetation was assessed at three levels of scale: in the 1 m^2 circular plot, in the 1 dm^2 seedling plot, and at the growing point. The first scale was assessed in the end of the first and fifth growing seasons for the 1996-cohort, and the two last ones in the end of the second growing season. Some information was lost, as the vegetation close to the seedlings that disappeared before the autumn of 1997 is unknown. Because the vegetation data was collected one or two growing seasons after germination, it is suitable for evaluating emergence- and establishment substrates rather than germination substrates. For most species, however, the changes in cover from 1996 to 2000 are relatively small (Table 2). Thus, the data collected in 1997 probably gives a good picture of the species present in the seedling plots and at the growing points in 1996.

Seedlings were counted each autumn and new ones were registered also in 1998, 1999 and 2000. In the summer of 2000, the microrelief in each 1 m^2 circular plot was registered as percent cover of each microrelief class. A plastic net with square openings of 1 dm^2 was used to aid the microrelief registration.

2.5. Data analysis

Changes from 1996 to 2000 in the cover of bottom- and field layer species in circular plots were analysed using a *t*-test for pairwise data. This test was also used for testing differences in vegetation between seedling- and circular plots around plants. If there were several seedlings within a circular plot, the vegetation data for the seedling plots was pooled before the test. A regular *t*-test was used for analysing differences in vegetation between circular plots with and without seedlings. Pearson correlation coefficients were computed for the cover of species in 1996 and microrelief classes in the circular plots. An analysis of variance for seedling emergence vs. year (1996–2000), site, and location (Ringkollen and Solør) was conducted using the model $Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_{k(j)}$, where Y_{ijk} is the number of emerged seedlings, μ the mean value, α_i the effect of year, β_j the effect of location and $\gamma_{k(j)}$ the effect of site within location.

Spearman Rank Correlation was computed for the number of spruce seedlings in each circular plot against cover of different vegetation species and microrelief classes. The relationship between the humus layer thickness and the number of seedlings emerged was investigated using simple linear regression. To test for long-term survival according to substrate, a chi-square test for survived vs. dead seedlings in 2000 was computed. Seedlings from 1996 were then placed in three groups, according to the vegetation at the growing point. The groups were (1) mosses (*Dicranum* spp., *H. splendens*, *P. crista-castrensis* and *P. schreberi*), (2) *Sphagnum*-mosses (mostly *S. girgensohnii*, some *S. capillifolium*) and (3) litter.

Seedlings that emerged in other types of vegetation were omitted in this analysis.

A one-way analysis of variance was conducted for the effect of distance to the seed tree edge on the number of emerged seedlings, with pairwise *t*-tests between treatment means. A test for the importance of direction to the remaining stand was conducted using data from circular plots up to 7.5 m from the edge in a covariance analysis, with site and direction as treatments and *Sphagnum* cover as a covariate. All calculations were executed using SAS software (SAS, 1989).

3. Results

3.1. Establishment and survival

All together, 403 seedlings and saplings were registered on the 251 circular plots. Of these, 382 (95%) appeared in 1996 (Table 4). The effect of year was significant in the analysis of variance (d.f. $= 4$, $F = 7.19$, $P = 0.003$), whereas the effects of site and location were not ($P > 0.30$). Of the circular plots 102 (40.6%) had one or more spruce seedlings in the autumn of 1996. In 2000, the number had decreased to 51 (20.3%).

Mortality of seedlings emerged in 1996 declined as time went by (Fig. 3). In September 2000, 140 seedlings were still present, 123 of these germinated in 1996. Of the 263 dead seedlings, 53 were found, the rest were not recovered.

Table 4
Year of emergence for the 403 seedlings found in the study and percent of circular plots with live seedlings

Year of germination	Number of seedlings	Percent	Percent circular plots with live seedlings ($n = 251$)
Advance regeneration	6	1.5	2.4
1995	3	0.7	2.8
1996	382	94.8	40.6
1997	5	1.2	29.5
1998	0	0.0	25.1
1999	7	1.7	23.1
2000	0	0.0	20.3
Sum	403	100.0	

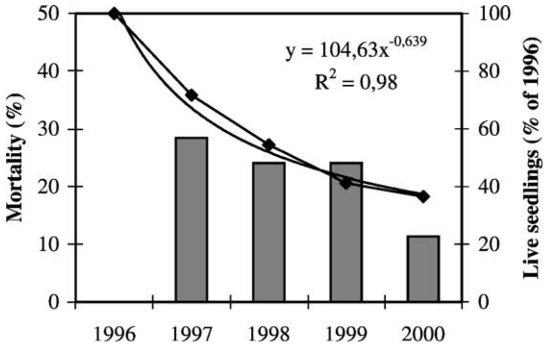

Fig. 3. Yearly mortality (bars) and survival (solid line with squares) of seedlings germinated in 1996. Survival in percent of seedlings alive in September 1996. The smooth solid line is a fitted regression curve.

3.2. Vegetation and humus

Although several species had a statistically significant change in cover between 1996 and 2000, only a few species actually changed more than 2–3% on average (Table 2). *D. flexuosa* had the largest increase, while *Dicranum* spp. had the strongest decrease.

A large percentage of the registered seedlings established in litter (48.1%) or *Sphagnum girgensohnii* (40%), even though these substrates only covered 11.6 and 5.0% of the ground, respectively (Table 5). Very few seedlings occurred in feather mosses (*H. splendens*, *P. schreberi* and *Ptilium crista-castrensis*) or *D. flexuosa*. The seedlings that died and disappeared

Table 5
Distribution of seedlings on different substrates at the growing point

Species/ substrates	No. of plants	Percent of plants	Mean cover of species, circular plots
Litter	137	48.1	11.6
S. girgensohnii	114	40.0	5.0
Dicranum spp.	14	4.9	20.1
P. commune	4	1.4	0.4
P. schreberi	4	1.4	7.5
Sphagnum capillifolium	3	1.1	0.5
D. flexuosa	3	1.1	40.6
H. splendens	1	0.4	2.0
B. lycopodioides	1	0.4	0.4
Other substrates	4	1.4	
Sum	285	100.0	89.5

Table 6
Difference in vegetation in circular plots (1 m^2) with ($n = 106$) and without ($n = 145$) spruce seedlings, and differences between seedling plots (1 dm^2) and circular plots around plants[a]

Species/substrates	Cover of species/substrates (%)			*t*-Tests (significant level %)	
	Seedling plots	Circular plots with seedlings	Circular plots without seedlings	Between circular plots	Between seedling- and circular plots
V. myrtillus	7.2	14.2	16.5	n.s.	0.001
V. vitis-idaea	1.1	1.8	3.4	0.05	n.s.
D. flexuosa	18.3	40.2	40.8	n.s.	0.001
Dicranum spp.	10.4	15.8	23.3	0.05	0.05
P. schreberi	1.1	7.5	7.6	n.s.	0.01
H. splendens	1.8	1.9	3.1	n.s.	n.s.
Sphagnum spp.	12.1	9.1	2.3	0.01	n.s.
P. commune	1	0.8	0.1	0.05	n.s.
Litter	47.9	11.9	11.4	n.s.	0.001
Branches	4.4	7.9	6.3	n.s.	n.s.

[a] *P* values for differences are calculated with *t*-tests. Species included in the table cover more than 1% of the ground, or express significant differences in the test.

before September 1997 are omitted in this table, as the vegetation at their growing points is unknown.

Circular plots *with* spruce seedlings had significantly more *Sphagnum* spp. and *Polytrichum commune* and less *Vaccinium vitis-idaea* and *Dicranum* spp. than plots where seedlings were absent (Table 6). For the rest of the species, the differences were insignificant. When testing the vegetation in the seedling plots against the larger circular plots, there was significantly less *V. myrtillus*, *D. flexuosa*, *Dicranum* spp. and *P. schreberi* close to the seedlings, while the percentage of litter was much larger (Table 6). A Spearman Rank Correlation test between number of spruce seedlings and cover of different plant species in the circular plots (Table 7) gave much of the same result: *Sphagnum* spp. and *P. commune* were positively correlated with the number of spruce seedlings, while *V. vitis-idaea* and *Dicranum* spp. were negatively correlated.

Seedlings that established in litter (recorded at the growing point in 1997) had slightly better long-time survival than those establishing in *Sphagnum* or other mosses (Fig. 4). Less than 40% of the seedlings established in mosses were alive in September 2000. The differences were not, however, significant when tested with a chi-square test ($P = 0.10$).

The number of seedlings in each circular plot were found to be positively correlated with humus depth, even though the coefficient of determination is small ($P = 0.05$, $R^2 = 0.06$).

Table 7
Spearman Rank Correlation between number of spruce seedlings in the circular plots and the distance to seed trees, cover of microrelief and cover of vegetation[a]

	Spearman Rank Correlation	Significant level %
Distance from seed trees (m)	−0.24	0.01
Microrelief groups		
Level ground	0.06	n.s.
Sloping ground	−0.08	n.s.
Depression	0.09	n.s.
Elevation	0.01	n.s.
Vegetation		
C. vulgaris	0.01	n.s.
D. flexuosa	−0.05	n.s.
Dicranum spp.	−0.15	0.05
H. splendens	−0.08	n.s.
Litter	0.04	n.s.
P. schreberi	−0.08	n.s.
P. commune	0.25	0.001
R. idaeus	0.17	0.01
S. capillifolium	0.13	0.05
S. girgensohnii	0.31	0.001
V. myrtillus	−0.04	n.s.
V. vitis-idea	−0.22	0.001

[a] Species included in the table cover more than 1% of the ground, or express significant differences in the test.

3.3. Microrelief

Although depressions occupied only 4.9% of the area, 24.1% of the seedlings established here (Table 8).

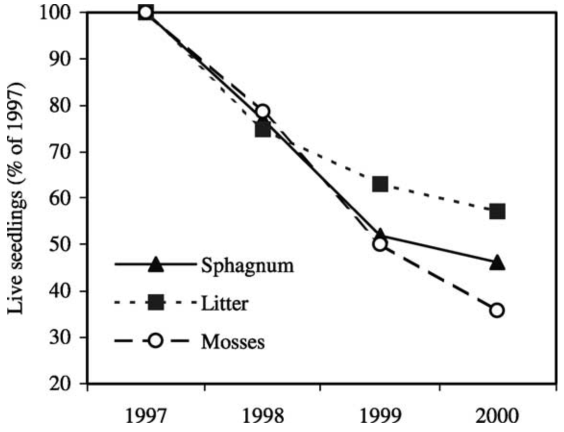

Fig. 4. Survival on different substrates for the 1996 cohort. Data for seedlings alive in September 1997.

Sloping ground occupied 40.8%, but only 19.5% of the seedlings occurred there. However, it seems that survival was slightly better on sloping ground, as 23.3% of the seedlings alive in the autumn of 2000 grew here, while only 19.6% grew in depressions. For level ground and elevations, the plant establishment about equals the presence of these microrelief classes. When tested with the Spearman Rank Correlation, the cover of the microrelief classes in the circular plots did not show significant correlations with the number of spruce seedlings (Table 7). The cover of some of the species, for instance *Sphagnum*, *V. myrtillus*, *D. flexuosa* and *P. schreberi*, were significantly correlated with some of the microrelief groups (Table 2). No species were found to correlate with the amount of depressions in the circular plots.

3.4. Distance and direction from seed trees

The analysis of variance showed that the distance from the surrounding forest edge had a significant influence on the number of spruce seedlings ($P = 0.005$). The average number of plants per circular plot decreased with increasing distance to seed trees up to 12.5 m, then increased slightly (Fig. 5, grey bars).

Table 8
Cover of microrelief classes in the circular plots, and occurrence of seedlings in the different classes

Microrelief	Total cover (%) ($n = 251$) ± 1S.E.	Occurrence of seedlings 1996–1999 (%) $n = 282$	Seedlings alive 2000 (%) $n = 133$	Seedlings dead by 2000 (%) $n = 149$
Level ground	43.6 ± 2.1	50.0	51.1	49.0
Sloping ground	40.8 ± 2.0	19.5	23.3	16.1
Depression	4.9 ± 0.4	24.1	19.6	28.2
Elevation	7.3 ± 0.4	6.0	6.0	6.0
Other (root, stump, stones)	3.4 ± 0.1	0.4	0.0	0.7

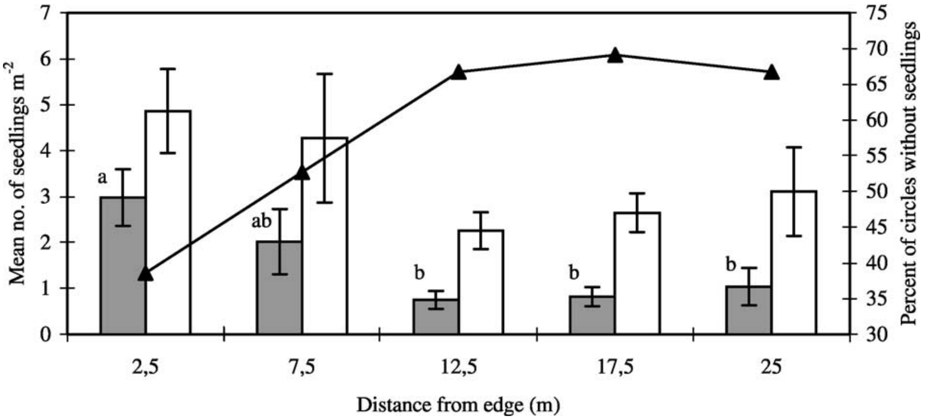

Fig. 5. Mean number of spruce seedlings per circular plot (1 m^2) at different distances from the edge of the remaining stand (grey bars), mean number of seedlings when circular plots without seedlings are left out (white bars) and percent of circular plots without seedlings (line). Error bars indicate the standard error. Different letters above bars indicate significant ($P \leq 0.05$) differences among treatment means.

The same trend is apparent when circles without seedlings are left out of the calculation (white bars). The percentage of circular plots without seedlings is lowest close to the remaining stand, increases up to 12.5 m and then levels off (solid line). Looking at the circular plots up to 7.5 m from the remaining stand, it was found that the average number of seedlings differed with direction to the closest stand edge, with more seedlings on the north and south side of the clear-cut than in the west and east. However, the cover of *Sphagnum* spp. varied in a similar manner, with more *Sphagnum* substrates in the north and south. When *Sphagnum* cover was added as a covariate, the differences between the sides were no longer significant.

4. Discussion

4.1. Regeneration dynamics

This study confirms that the occurrence of seed years is important to get natural regeneration of Norway spruce in southeastern Norway at middle altitudes. In the 6 years from the time of clear-cutting to the end of the study, there was one year with rich seed setting and good ripening conditions; 1995 (Table 3). The seeds from this year were the source of 95% of the found seedlings.

The seed year appeared 1 year (Ringkollen) and 2 years (Solør) after cutting. Some time-dependent vegetational changes that appear after cutting affect emergence and survival of seedlings, for instance the disturbance of the *P. schreberi*-layer right after cutting (Nilsson et al., 1996) or increase in the cover of species like *D. flexuosa* with time (Hertz, 1932; Granström, 1986; Skoklefald, 1992b). A longer time span from cutting to a good seed year can therefore affect the regeneration result negatively. However, the pine weevil (*Hylobius abietis* (L.)), which is an important cause of seedling mortality on clear-cuts, is more abundant on fresh clear-cuts (von Sydow, 1997; Örlander et al., 1997; Örlander and Nilsson, 1999).

Mortality for the 1996-cohort showed a decreasing trend, as the seedlings grew older (Fig. 3). Larger seedlings are less susceptible to drought, are better competitors for light and nutrients, and have better chances of surviving predator attacks, e.g. by pine weevils (Örlander and Nilsson, 1999; Thorsen et al., 2001). The available data does not give information about seedling mortality the first growing season. However, in a sowing experiment with Norway spruce seeds on the three clear-cuts at Ringkollen 1997–1999 on various seedbed substrates, mean mortality the first growing season (between the beginning of July and the end of September) was for all sites and years 34.2% ± 7.3 S.E. (unpublished data).

4.2. Vegetation

Although the results concerning the effect of the vegetation on seedling establishment and survival vary somewhat, some general trends are apparent. The occurrence of *Sphagnum* spp., litter and *P. commune* seem to be beneficial for establishment, while *D. flexuosa*, *Dicranum* spp. and *P. schreberi* seem to imply an environment inimical to seedlings. *V. myrtillus* was also seldom found around seedlings.

Sphagnum species, mostly *S. girgensohnii*, was found at the growing point of 40% of the seedlings (Table 5), and there was significantly more *Sphagnum* in circular plots *with* seedlings than in those without (Table 6). The number of seedlings in each circular plot was also positively correlated with the cover of *Sphagnum* spp. (Table 7). Long-term survival for the established plants was slightly better in *Sphagnum* than in the other mosses, but lower than in litter (Fig. 4). *Sphagnum* spp. are capable of taking and storing water from the atmosphere, and have great capillary forces (Du Rietz et al., 1952). Thus, they create a suitably humid environment for germination and establishment, and the importance of *Sphagnum* spp. as a suitable emergence substrate has been found in several studies (Ohlson and Zackrisson, 1992; Jeglum and Kennington, 1993; Fleming and Mossa, 1994; Hörnberg et al., 1997). However, *Sphagnum*-mosses are known to overgrow small seedlings of spruce and pine (Groot and Adams, 1994; Ohlson, 1995). Pakarinen and Rinne (1979) found that *S. girgensohnii* shoots could grow up to 10 cm in one year. Consequently, the seedlings have to increase in length more than the *Sphagnum* to survive; otherwise they will be smothered by the moss. This smothering was also observed in the present study. Thus, the seedling survival in *Sphagnum*-mosses can be low in the long run.

Litter was the most common substrate at the growing points and in seedling plots (Tables 5 and 6), and had the highest survival. Litter is generally considered to be a poor seedbed, especially if found in thick layers (Nakamura, 1992; Jeglum and Kennington, 1993; Groot and Adams, 1994). The reason for this is fast evaporation and potential for very high temperatures in litter, and possible allelophatic impacts from decomposing spruce needles on germination and seedling growth (Pellisier, 1993; Gallet, 1994; Gallet and Lebreton, 1995). Caccia and Ballaré (1998) found that irrigation partially counteracted the negative impact of thick litter layers on seedling emergence of *Pseudotsuga menziesii*, and they suggested that it is the interaction between depth of litter layer and water availability at seed level that determines initial seedling survival and emergence. Herr et al. (1999) came to the same conclusion for *Pinus strobus*. Competition from other species is less severe in areas dominated by litter, and nutrient levels can be high due to decomposition of organic substances. Often, the litter found at the growing point of the seedlings only covered a few square cm, in between different kinds of vegetation. Thus, the litter layer would have a modest thickness, and often be shaded by nearby vegetation. In 1996, when most seedlings germinated, May was a fairly wet month, and there were no long lasting dry spells in June. Under such conditions, litter might represent a good seedbed. Once the radicle has reached soil layers with more stable moisture supply underneath the litter layer, periods of drought will have less impact on survival. The findings of this study were confirmed by a sowing experiment (Hanssen, 2002), where litter was found to be a reasonably good substrate for seedling establishment.

P. commune prefers moist conditions (Hallingbäck and Holmåsen, 1991). It is also a pioneer species, and was often observed establishing in the scarified spots on the clear-cuts used in this study. As the occurrence of *P. commune* is small in the studied areas, it is difficult to draw conclusions about its suitability as an establishment substrate for spruce. However, the connection to moist conditions makes it likely that areas with *P. commune* could be acceptable for establishment and survival of seedlings, as was found by Jeglum and Kennington (1993) for black spruce (*Picea mariana* (Mill)). As this moss can reach a height of 30 cm, it can probably become a serious competitor to spruce seedlings, as claimed by Hertz (1932) and Skoklefald (1992b). Further studies are needed to determine the suitability of the species for establishment and survival of seedlings.

There was significantly less *P. schreberi* in the nearest vicinity to the seedlings compared to the wider circular plots (Table 6). Very few seedlings actually established in *P. schreberi* or the other feather mosses (Table 5), and seedling survival was also low (Fig. 4). Zackrisson et al. (1997, 1999) found that *P. schreberi* had the ability to block the nutrient uptake of Scots pine (*Pinus sylvestris*) seedlings, especially in association with ericaceous plants and fungal hyphae. Steijlen et al. (1995) found that allelopathy also may be the reason for low germination of Scots pine seeds in *P. schreberi*, and they concluded that moisture, chemical interference and barriers of nutrient availability all appeared to inhibit early pine establishment in this seedbed substrate. However, Nilsson et al. (1996) found that *P. screberi*-dominated microsites could constitute a favourable microhabitat for pine regeneration following stand disturbance, but the positive effect quickly diminished with time after disturbance. In an experiment with different seedbed substrates, Oleskog and Sahlén (2000) determined that moisture conditions for germination of *P. sylvestris* were most favourable on mineral soil, and least on intact feather mosses and humus. Also Wood and Jeglum (1984) found that *P. schreberi* forms a seedbed too dry for successful regeneration. The contact between seed and substrate can be insufficient on feather mosses, and evaporation can be fast, making moisture conditions bad for germination (Brown et al., 1988; Bonan and Shugart, 1989). It is probable that moisture conditions, nutrient blocking and allelopathy all contributed to restricting spruce establishment in the present study.

Dicranum spp. seems to be even a poorer seedbed than feather mosses (Tables 5–7). This probably reflects the fact that these mosses (mostly *D. scoparium* and *D. polysetum*) mainly grow in dry places, on shallow and stony ground. As for *P. schreberi*, the evaporation is probably fast, and contact between seed and substrate is poor.

Wavy hair-grass (*D. flexuosa*) is known to grow vigorously on clear-cuts in bilberry woodlands. There are many records of how *D. flexuosa* prevents the germination and growth of conifer seedlings, e.g.

Hertz (1932) and Skoklefald (1992b). A seedling will experience heavy competition for water and nutrients when the radicle tries to penetrate the thick mat of roots in a *D. flexuosa* community. The mechanical pressure from dead straws can also be a threat, bending and eventually smothering a young seedling. Lekander and Söderström (1969) found that predation by *H. abietis* was more intense in grass covered areas than in mosses or on mineral soil. Nilsson and Örlander (1999) conclude that the competition between grasses such as *D. flexuosa* and planted seedlings mainly involves processes occurring below ground. The situation might be different for seedlings established from seeds, as they initially are smaller and less capable of competing for light.

There was less bilberry (*V. myrtillus*) in the seedling plots compared to the circular plots (Table 6). Dense populations of bilberry effectively prevent germination and establishment of conifers (Skoklefald, 1992b), through belowground competition (Jäderlund et al., 1997), and probably through allelopathy (Pellisier, 1993; Gallet, 1994; Gallet and Lebreton, 1995), even though Jäderlund et al. (1996) found phytotoxicity from bilberry unlikely to be of critical importance in determining success for spruce seedling establishment.

The vegetation closest to the seed or seedling is likely to have the greatest influence on emergence and survival, even though the species vigour and size (both above- and belowground) must be considered too. The results concerning the vegetation around seedlings give some indications of the importance of scale. Some species tend to differ on the 1 m^2 scale, between circular plots with and without seedlings. There is more *Sphagnum* spp. and *P. commune*, and less *V. vitis-idea* and *Dicranum* spp. in the plots with seedlings. These species can be said to be indicators of the amount of *moisture* in the area—either plenty (the two first species) or little (the two last species). As moisture is an environmental condition that may range over a scale of several square meters, it seems logical that these indicator species differ on a "large" scale, i.e. between circular plots. Other species/substrates are found in equal amounts in circular plots both with and without seedlings, but are more abundant (litter) or scarce (*V. myrtillus*, *D. flexuosa*, *P. schreberi*) in the close vicinity of the seedlings (seedling plots, 1 dm^2) than in the larger circular plots. *Dicranum* seems to matter on both scales (Table 6). These latter species/substrates can exist under a wide range of moisture conditions, and express good or bad germination conditions more dependent on "innate" properties that will affect the seed or seedling locally: severe competition (*D. flexuosa*, *V. myrtillus*), allelopathy (*P. schreberi*, *V. myrtillus*), surfaces that dry out easily (*P. schreberi*, litter), nutrient lockup (*P. schreberi*), and absence of competitors (litter).

4.3. Humus layer

The positive, although weak relationship between thickness of the humus layer and number of emerged seedlings is contrary to the findings in other studies (Skoklefald, 1965; Caccia and Ballaré, 1998; Herr et al., 1999). A thick humus layer is considered negative for regeneration, because it takes the seedlings a long time to grow roots into the mineral soil, which provides a more stable moisture regime. However, it was noted that some of the driest plots on the five clear-cuts, on ridges or stony ground, often had very thin humus layers. The vegetation in these places was usually constituted by species like *V. vitis-idaea* and lichens. Even though the humus layer is thin enough here for the seedlings' roots to reach mineral soil quickly, the soil is probably to dry for survival. More humid microsites with plentiful vegetation have thicker humus layers, but might also supply enough water for the seedling to survive until their roots reach the mineral soil. Larsson et al. (1997) stress that other properties of the humus layer, for instance humus form, is important when assessing the influence of the humus layer on regeneration. They consider bilberry woodland as one of the vegetation types with greatest variation in humus forms. Further studies are required to assess the effect of other properties of the humus layer.

4.4. Microrelief

Hörnberg et al. (1997) and Gunnarsson and Rydin (1998) studied seedling emergence and survival in peatlands, and found that elevated sites had more seedlings than hollows. In mineral soil, the significance of the microrelief will be quite the opposite from peatlands: conditions that enhance the moisture content in the soil will usually be positive, as lack of moisture often restricts germination and establishment of spruce in Norway (Bjor, 1971; Skoklefald, 1992b). Better moisture conditions are probably the main reason for the high occurrence of seedlings in depressions in this study (Table 8). Depressions are closer to the water table, and runoff water will congregate in hollows. Seeds may also be washed down into depressions by heavy rain. Filion and Morin (1996) found that seedlings of *P. mariana* in a burnt area were mostly associated with concave microsites. The reason why long-term survival was lower in depressions might be that the favourable moisture conditions also lead to vigorous growth of other plant species, causing heavy competition. Mortality caused by inundation will also be higher in depressions.

Sloping ground had fewer seedlings than its cover would imply. Water runs off quickly on sloping ground, and dry spells can therefore appear more frequently. The low occurrence of seedlings on sloping ground is most likely a combination of microrelief and vegetation cover, as sloping ground was negatively correlated to *Sphagnum*-mosses and positively to *V. myrtillus* on the 1 m^2-level (Table 2). However, it was also negatively correlated with the amount of *D. flexuosa*, which should imply better conditions for the seedlings.

4.5. Distance to seed trees

As the distance from the seed trees increase, the number of seeds reaching the ground decreases. Spruce seeds are relatively heavy compared to many deciduous species (e.g. *Betula* and *Alnus*), and fall to the ground within one to two treelengths from the mother tree (Hesselman, 1938). The seeds falling far from the mother tree have a higher percentage of empty seeds, and even the filled seeds tend to be lighter, and thereby of a lesser quality. Other studies have also found a decreasing number of seedlings with increasing distance from seed trees, both for Norway spruce (Hanssen, 1996) and for other conifer species (Skoklefald, 1992a; Galipeau et al., 1997; Asselin et al., 2001). Reduced evaporation due to shading might be another reason for better emergence and seedling survival in the vicinity of seed trees. However, as direction to the remaining stand did not matter in this study, the availability of seeds seem to be the dominating cause to the higher seedling emergence close to the seed trees.

5. Conclusions

Litter, *Sphagnum* spp. and *P. commune* were found to be good substrates for seedling emergence. Very few spruce seedlings established in *D. flexuosa*, *Dicranum* spp., *V. myrtillus* or *P. schreberi*. Establishment after five growing seasons suggest a somewhat better survival in litter than in *Sphagnum* and other mosses. Increasing humus depth was found to have a positive influence on regeneration. More seedlings established in depressions than would be expected from the distribution of this microrelief group, and less on sloping ground. However, 5-year survival was slightly better on sloping ground, and lowest in depressions. Literature reviews imply several possible reasons for the suitability or unsuitability of the microhabitats. Factors connected to moisture (competition, seed–substrate contact, risk of substrate desiccation) are crucial, but allelopathy, nutrient availability and predation may also be important causes. The amount of seedlings was highest close to the surrounding stand, showing that distance to seed trees matter also on small (50 m wide) clear-cuts.

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