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Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting

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Abstract

Clearcutting and shelterwood cutting of mature Norway spruce peatland forests were compared regarding the effects on the forest flora. Repeated observations of the field and bottom layer vegetation were made before and until 7 or 8 years after harvesting at four sites located along a gradient from southern to northern Sweden. Clearcutting resulted in a greater change of species composition compared with shelterwood cutting. Diversity, measured as Simpson's index, and species number per subplot were lower in the clearcut than in the shelterwood after 7 or 8 years. By applying Ellenberg's indicator values, it was concluded that shelterwood regimes may preserve species preferring shaded and moist conditions, whereas those species decreased after clearcutting. Species preferring high levels of nitrogen increased in the clearcut.

According to both multivariate and univariate analyses, the vegetation changed in a similar direction at all sites, although the level of response differed considerably. Despite these similarities, there was a marked site effect, which was not surprising considering the large geographic variation between sites.

It is concluded that shelterwood cutting might be a better alternative than clearcutting for forests on fertile peatland sites, with respect to conservation of vascular plants and bryophytes.

Keywords: Vegetation; Flora; Succession; Peatland; Clearcut; Shelterwood; Diversity; Ellenberg indicator values

1. Introduction

Clearcutting is a major disturbance in a forest ecosystem, with large impacts on hydrologic, biogeochemical and other processes (Likens et al., 1978). Solar radiation, temperature amplitudes and wind velocity usually increase, while humidity decreases. Other expected consequences are faster litter decomposition, increased amounts of available nutrients, and increased soil water content (Röhrig and Gussone, 1982; Hannerz and Gemmel, 1994). After clearcutting the flora is converted from late successional to early successional species (Huston, 1994), and a number of plant species may even become extinct at a site after clearcutting. Clearcutting is expected to negatively affect as many as 550 threatened red-list species (animals and plants) in Sweden (Bernes, 1994). Of these, Hallingbäck and Lennartsson (1994) estimate that 39 vascular plant species are threatened by clearcutting.

In northern boreal forests, the level of the impact

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caused by clearcutting is related to the forest type and disturbance history. Fire is the major disturbance factor (Zackrisson, 1977), and the degree of fire-influence has been used to create a model for forestry practices in boreal ecosystems (Rülcker et al., 1994). In this model it is proposed that sites adapted to frequent fire disturbances can be harvested with methods resembling clearcutting without harming the biological diversity, provided that important structures such as green trees and dead wood are left. In contrast, forests on sites that never or seldom have been exposed to fire should not be harvested at all, or should be harvested with selective methods.

Since the beginning of the 1950s, clearcutting has been the dominant harvesting method in Sweden (Bernes, 1994). However, during the last decade there has been an increased use of harvesting methods that never leave the ground completely bare. There are several incentives behind this trend, one of which an increased awareness of biodiversity. This is expressed in the Swedish Forestry Act of 1993, where wood production and biodiversity are given equal importance (SOU, 1992). Another important factor is economy. On moist and frost-prone sites, regeneration after clearcutting has often led to failures resulting in high replanting costs (Hånell, 1992). As a consequence, shelterwood regeneration of spruce forests has increased in popularity during recent years. In some regions, as much as 15–20% of the spruce regeneration is performed with shelterwood systems (Westerberg, 1995), but on a national level these systems are only practised on a relatively small scale. In 1993, shelterwood cuttings were carried out on approximately 5% of the regenerated spruce area (Hörnsten, 1995). The shelterwood reproduction method involves the gradual removal of a stand in a series of partial cuttings at the end of the rotation. Natural regeneration starts under the protection of older (shelter) trees and is finally released when able to endure exposure. The most fundamental characteristic of the shelterwood method is the establishment of a new crop before completion of the preceding rotation (Hawley and Smith, 1954). Shelterwood systems make it possible to overcome some of the above-mentioned disadvantages that are typical of clearcutting (Ottosson-Löfvenius, 1993; Hannerz and Gemmel, 1994).

It is highly desirable to determine the effects of different harvesting regimes on biodiversity. The regrowth and early succession of the flora after clearcutting has been subjected to many studies (Dyrness, 1973; Ingelög, 1974; Outcalt and White, 1981; Gholz et al., 1985; Schoonmaker and McKee, 1988; Zobel, 1989, 1993; Olsson and Staaf, 1995). However, very few comparisons have been made of different harvesting regimes as to their effects on the flora in coniferous boreal forests (Kardell and Eriksson, 1983; Gove et al., 1992; Hannerz and Hånell, 1993).

This paper is focused on the effects on forest flora following shelterwood cutting and clearcutting. The studies were performed at four experimental sites representing spruce forests on fertile peatlands in south, central and north Sweden. The experiments were established in 1985–1987 (Hånell, 1993). The flora was surveyed from the year before harvesting until seven–eight years after harvesting. Observations from 5 years after cutting have been reported by Hannerz and Hånell (1993). That study was restricted to observations of the vascular plant species at one study site. This paper reports the compiled results on vascular plants and bryophytes at the four sites. It also includes an indirect comparison of environmental variables between shelterwood cutting and clearcutting by the use of indicator values (Ellenberg et al., 1991).

2. Materials and methods

2.1. Experimental sites

Four experimental sites on fertile peatlands (5–20 ha) dominated by Norway spruce (*Picea abies* (L.) Karst.) were included in the study (Table 1, Fig. 1). The sites were drained more than 50 years before this study. The site type was classified as *Maianthemum-Viola*/low-herb type (Hånell, 1991a,b). The study was restricted to parts of the experimental sites where no post-harvest silvicultural treatments had been carried out.

The canopy of the spruce stand of the southernmost site, Mogård, was fully closed. The field layer was very sparse and dominated by *Trientalis europaea*, *Vaccinium myrtillus* and *V. vitis-idaea*.

Table 1
Study site information

Site	Mogård	Labbaliden	Fallet	Stormora
Site				
Latitude (°N)	57°05′	57°21′	60°30′	64°13′
Longitude (°E)	13°24′	14°23′	17°11′	20°45′
Altitude (m asl)	145	210	45	75
Temp sum (dd)	1350	1300	1300	1000
Peat depth (cm)	83	129	130	49
Nitrogen [a]	1.95	2.13	2.54	1.10
Phosphorus [a]	0.08	0.09	0.09	0.09
Potassium [a]	0.02	0.02	0.04	0.07
Water table (cm) [b]	10	60	65	50
Indicator value [c]				
Light	4.96	–	4.11	4.23
Moisture	4.44	–	5.41	6.19
pH-reaction	2.30	–	4.26	3.79
Nitrogen availability	2.59	–	4.39	3.54
Stand				
Trees (ha^{-1})	1440	995	656	538
Pine–spruce–birch	1–8–1	0–10–0	0–10–0	0–10–0
Stand volume (m^3 ha^{-1})	287	225	381	218
Measures				
Harvesting	Nov 1986	Dec 1986	May 1987	Apr 1986
Ditch cleaning	Apr 1987	Apr 1987	–	Oct 1986

[a] Content in the peat, 0–40 cm. Per cent of dry weight (sampling methods described in Hånell, 1991b).
[b] Average ground water table at the sites in July 1987 (detailed figures in Hånell, 1992).
[c] Mean indicator value (Ellenberg et al., 1991) in all treatments before harvesting. Calculated from species frequency in subplots.

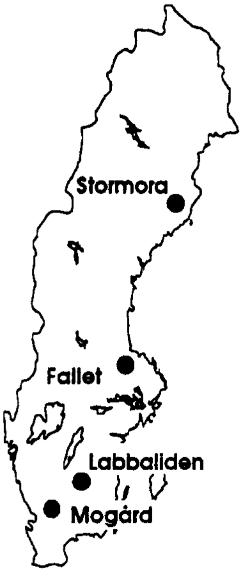

Fig. 1. The study sites.

Bryophytes covered less than 40% of the ground, with *Dicranum* spp. and *Pleurozium schreberi* as the dominant species. Labbaliden also had a sparse field and ground layer. *Dryopteris carthusiana, Oxalis acetosella* and *V. myrtillus* were the most dominant vascular plant species, and *Brachythecium* spp., *Dicranum* spp. and *P. schreberi* were the most common bryophytes. In spots where the canopy was less dense the vegetation was richer. Beside the dominant species, *Lactuca muralis, Maianthemum bifolium, Rubus idaeus* and *T. europaea* occurred frequently. Fallet was the most species-rich and fertile of the sites in this study, with *D. carthusiana* and *O. acetosella* as dominant vascular plant species. Other common species, indicating high fertility, were *Hepatica nobilis, L. muralis, Milium effusum, Paris quadrifolia* and *Urtica dioica*. The most common bryophytes were *Brachythecium* spp., *Dicranum* spp. and *Plagiochila* spp. The vegetation in the major part of the northernmost study site, Stormora, was species-rich and indicated fertile conditions (*O. acetosella, D. carthusiana, Equisetum sylvaticum* and *Calamagrostis purpurea*). In a small part of the site *Carex globularis, Rubus chamaemorus* and *V. myrtillus* were the most characteristic species, indicating poor and wet conditions.

2.2. Experimental design

Each site was divided into two parts; one part was clearcut and in the other part a shelterwood was left. At each site clearcut was represented by two plots (40 × 25 m) and shelterwood by four plots (20 × 25 m). At the Stormora site, four and eight plots were established on clearcut and in shelterwood, respectively.

Two shelterwood treatments, 140 and 200 trees per hectare, were tested in the experiments. Due to windthrow, the number of shelter trees was reduced (Table 2), and the difference between the shelterwood densities became smaller. Most of the windfall occurred during the first 2 years after cutting (see Hånell and Ottosson-Löfvenius, 1994). It was not relevant for this particular study to separate between dense and thin shelterwoods. Instead, they were combined into one treatment.

2.3. Measurements

Observations on the cover of vascular plant vegetation were made before cutting (1985 and 1986), 1 year after (1987), and 7 or 8 years after cutting (1993) (Table 3). At one site, Fallet, observations were also made 5 years after cutting (1991). The bryophyte flora was measured in 1985 and 1993 at three sites. Bryophytes were identified to species level where examination in the field was possible. In other cases they were identified only to genera. Labbaliden was assessed only in 1993 regarding both vascular plants and bryophytes. All vegetation observations were made in temporary subplots systematically distributed in the plots (described in Hannerz, 1988). Subplot size was 1 × 1 m in the inventories until 1991 and 0.5 × 0.5 m in 1993. With the exception of 1985, 12–30 subplots were used in each plot, corresponding to 24–160 subplots per treatment and site (Table 3). All inventories in all years were made by the first author. Nomenclature follows Krok and Almqvist (1991) for vascular plants and Hallingbäck and Söderström (1987) for bryophytes.

In each subplot the cover of horizontal projection (%) was estimated for each species. Cover was registered in the following classes: 0.01, 0.02,..., 0.04, 0.05, 0.1, 0.5, 1, 2,..., 9, 10, 15, 20, 25, 30, 40,..., 90, 100. A quadrat frame with each 10 cm marked was used. In 1993, the estimated mean height of all vascular plant species in each subplot was measured with the aid of a ruler.

Table 2
Remaining shelter trees per hectare at the study sites in 1993 (mean and variation between plots)

	'Dense' shelterwood	'Sparse' shelterwood
Stormora	95 (70–120)	107.5 (90–150)
Mogård	80 (20–140)	50 (40–60)
Labbaliden	205 (190–220)	155 (150–160)
Fallet	125 (100–150)	105 (90–120)

Table 3
Number of subplots at each inventory

Year after harvesting [a]	Clearcut	Shelterwood	Date of inventory
Mogård			
−1	12	8	Oct 15–16 1985
0	54	56	Sept 1 1986
1	42	48	Aug 19 1987
7	60	120	July 20 1993
Labbaliden			
7	60	119	July 21–22 1993
Fallet			
−1	6	20	Oct 10 1985
0	42	60	Aug 21–22 1986
1	42	48	Sept 10 1987
5	42	48	Aug 24 1991
7	40	90	July 23–29 1993
Stormora			
0	24	16	Sept 25–29 1985
1	96	112	Sept 19–23 1986
2	95	105	Sept 30 1987
8	80	160	July 26–28 1993

[a] '0' marks the summer/autumn before harvesting. Inventories at age '−1' are used here only to describe mosses before harvesting.

2.4. Data treatment

The average cover and frequency of single species were calculated plotwise for each inventory. Total cover of field layer and bottom layer, respectively, was calculated as the sum of single species cover. Diversity (D) was expressed with Simpson's index, $D = 1 - \Sigma p_i^2$, where p_i is relative cover for species i. Relative cover was calculated as single species cover divided by total cover in the subplot. Richness was expressed as number of species per subplot. Because of the reduced subplot size in 1993, time trends for diversity and richness over the entire study period could not be calculated.

At the Stormora site, one plot was excluded from the analysis, since the DCA-analysis (see below) revealed it to be an extreme outlier. The vegetation in the plot, mainly *C. globularis* and *R. chamaemorus*, indicated poor and wet conditions.

The environmental conditions were described by using indicator values for vascular plants set by Ellenberg et al. (1991). Each value indicates the optimum condition for a species with respect to a certain environmental variable. The variables focused on in this study were light, moisture, pH, and plant-available nitrogen. The indicator values range from 1 to 9 (moisture from 1 to 12). High and low values reflect high and low demands, respectively. In cases where indicator values were lacking or likely to not reflect the species preferences in Swedish conditions, values were adjusted or introduced based on information in Sjörs (1956), Gustafsson (1994) and Diekmann (1995) (see Section 4.3).

Mean indicator values were calculated for each subplot based on presence/absence as suggested by many authors (see Section 4).

2.4.1. Univariate analysis

Univariate analyses according to a randomized block model (model 1) with sites as blocks, were run for the measures total cover, diversity, richness, mean indicator values and cover of bryophytes and a selection of frequent vascular plant species. The analyses were performed to compare treatments on the basis of data from the most recent inventory (7–8 years after cutting). All sites were included. Differences between treatments were tested with Tukey's test. The analyses were run in the SAS General Linear Models procedure (SAS, 1987).

$$y_{ij} = \mu + a_i + b_j + e_{ij} \qquad \text{(model 1)}$$

where

a_i = fixed effect of treatment (i = 1,2)
b_j = fixed effect of site (j = 1,4)
e_{ij} = random residual effect

2.4.2. Multivariate analysis

Multivariate analyses were used to illustrate the combined effects of treatments. The analyses were run with the program CANOCO (ter Braak, 1987, 1988). Plot mean values from data collected from before and 7–8 years after cutting at all sites except Labbaliden were used. Square root transformed plot mean covers of species were regarded as dependent (species) variables. Plot mean indicator values were passively related as external variables to the ordination axes.

One analysis was run for all three sites combined. Only species occurring in at least two plots at all sites were included. First, a correspondence analysis (CA) was run on species data. The ordination resulted in a strong arch-effect (not shown). Consequently, a detrended correspondence analysis (DCA) was run to remove the arch-effect (Jongman et al., 1987). The length of the first axis was 3.54 standard deviation units, indicating that an unimodal model rather than a linear model should be used.

DCA were also run for each site. The length of the first axis varied from 2.0 to 2.7 for each single site, indicating linear responses to environmental axes. Subsequently, PCA was run on each site with indicator values passively related to the ordination axes as described above. In PCA, the ordination was scaled to give Euclidian distance biplots, and species and sample data were centered and standardized to mean = zero and variance = 1.

3. Results

3.1. Field vegetation cover and height

The total cover of the field layer decreased the first year after cutting at all sites, being most pro-

Table 4
Total cover, mean height, diversity and richness for vascular plant species at all sites 7–8 years after harvesting, and results from Tukey's test

Site	Total cover (%)		Mean height (cm)		Diversity, Simpsons index		Richness	
	Clearcut	Shelt.w.	Clearcut	Shelt.w.	Clearcut	Shelt.w.	Clearcut	Shelt.w.
Mogård	54.3	50.0	–	–	0.30	0.36	2.68	3.37
Labbaliden	35.5	35.6	15.9	20.5	0.17	0.29	1.95	2.68
Fallet	97.4	116.0	54.1	74.1	0.46	0.64	5.78	8.42
Stormora	72.1	96.2	33.0	36.8	0.54	0.61	6.21	6.66
Average, all sites	64.8	74.4	34.3	32.9	0.37	0.48	4.16	5.28
Tukey's test [a]		ns		ns		[b]		ns

[a] Tukey's test of differences between treatments (model 1). Significance level: ns = not significant, [b] = $P < 0.05$, [c] = $P < 0.01$, [d] = $P < 0.001$.

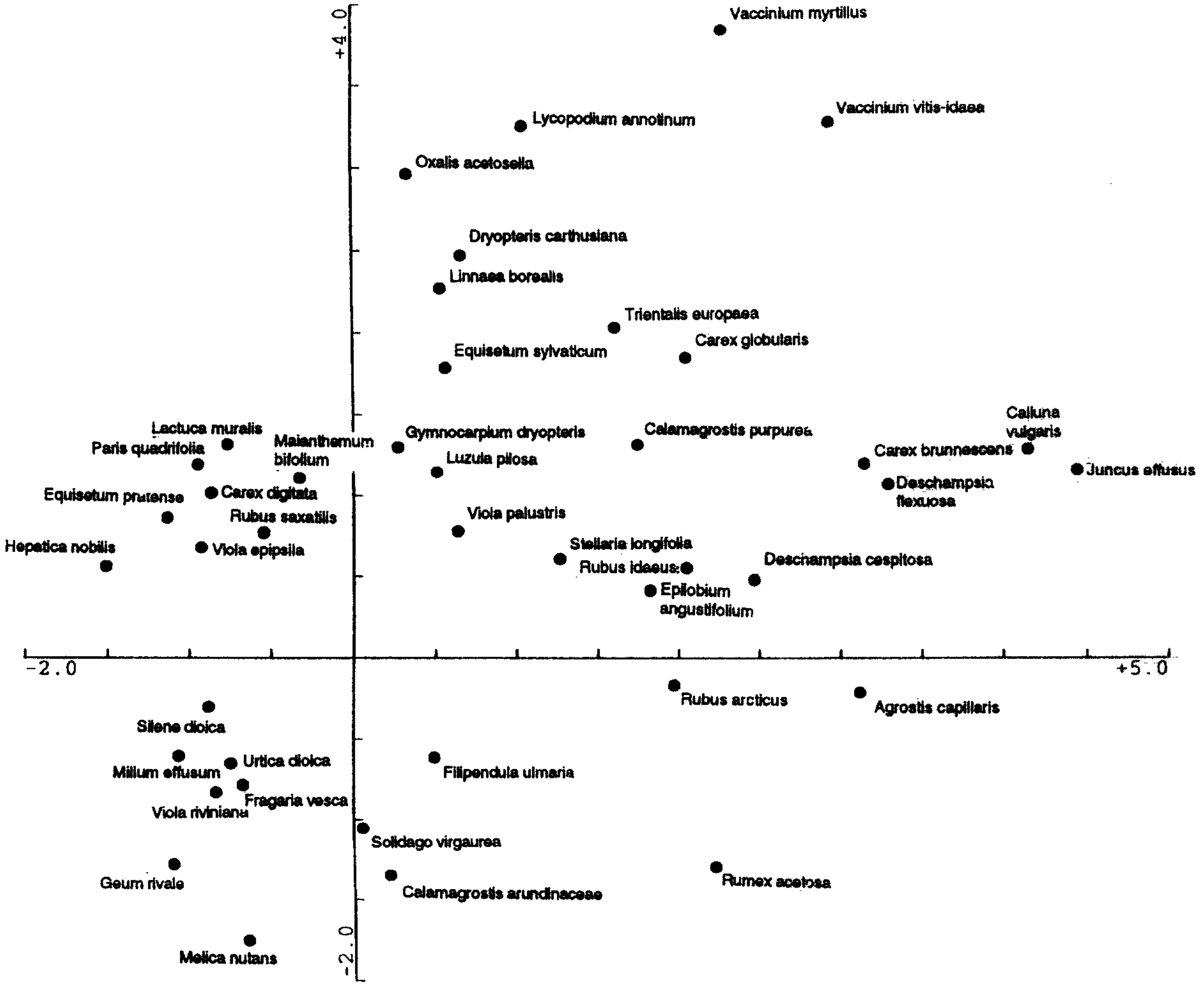

Fig. 2. Detrended correspondence analysis (DCA) ordination scatter of species, corresponding to the environmental variables/plots scatter of Fig. 3. Plot mean values from year 0 and years 7–8 from the sites Mogård, Fallet and Stormora of species occurring in at least two plots at all sites were included.

nounced on the clearcut. After 7 years it had increased considerably at all sites. The total cover was higher in the shelterwood than in the clearcut at two of the sites (Fallet and Stormora), and was almost the same at Mogård and Labbaliden. Also the mean height of the vegetation was higher in the shelterwood, thus expressing a higher density of field layer biomass compared with the clearcut (Table 4).

3.2. Diversity and richness

At all sites, diversity and richness were higher in the shelterwood than in the clearcut after 7–8 years, and the difference was significant according to model 1 for diversity (Table 4). A correct trend over time could not be calculated for all sites, as subplot size was reduced at the latest sampling occasion. At Fallet, both these variables increased considerably during the first five years in the shelterwood, whereas they remained the same in the clearcut (see also Hannerz and Hånell, 1993).

3.3. Multivariate analysis

The first two axes of the DCA for all three sites explained 32% of the variance for species data and 64% of the variance of species–environment relationship. The eigenvalue was 0.46 for the first axes

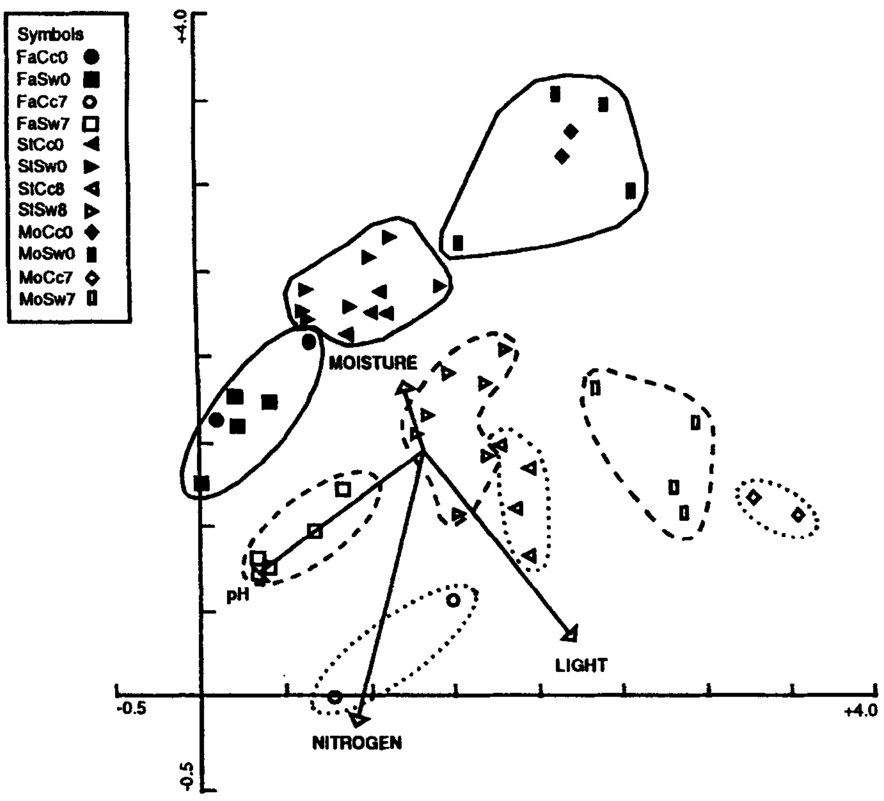

Fig. 3. Detrended correspondence analysis (DCA) joint-biplot of plots and passively related environmental variables. The arrows express gradients for the environmental variables, and the length of them the importance of the gradient. Encircled plots belong to the same site before and after harvesting. Solid line = all plots before harvesting, broken line = shelterwood after harvesting, dotted line = clearcut after harvesting. Symbol legends: Fa = Fallet, St = Stormora, Mo = Mogård, Cc = Clearcut, Sw = Shelterwood. 0 = the year before harvesting. 7(8) = 7(8) years after harvesting.

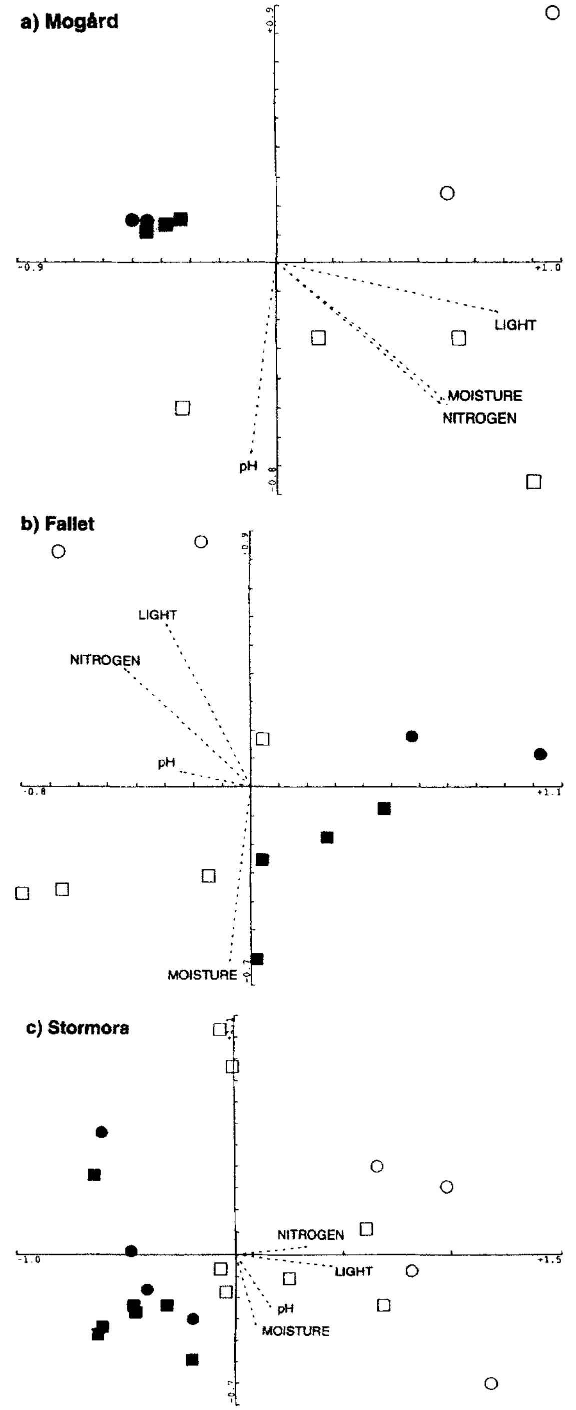

Fig. 4. (a–c). PCA biplots from the three individual sites (Mogård, Fallet and Stormora) with plots before (year 0 – filled) and after (year 7–8 – open) harvesting and passively related environmental variables. Circles are clearcut plots, squares are shelterwood plots.

and the sum of all unconstrained eigenvalues was 2.22.

The least nutrient-demanding species were found in the upper, right part of the ordination diagram, and those preferring fertile sites were mainly clustered in the lower left part (Fig. 2). This interpreta-

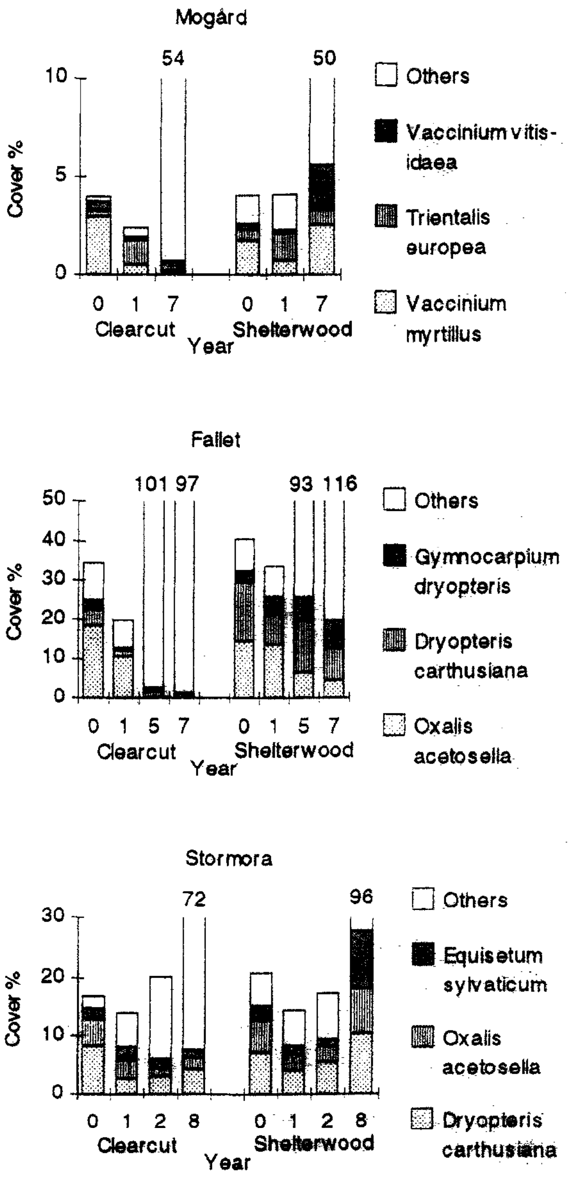

Fig. 5. Changes in cover of the three species that were most dominant before harvesting at each site.

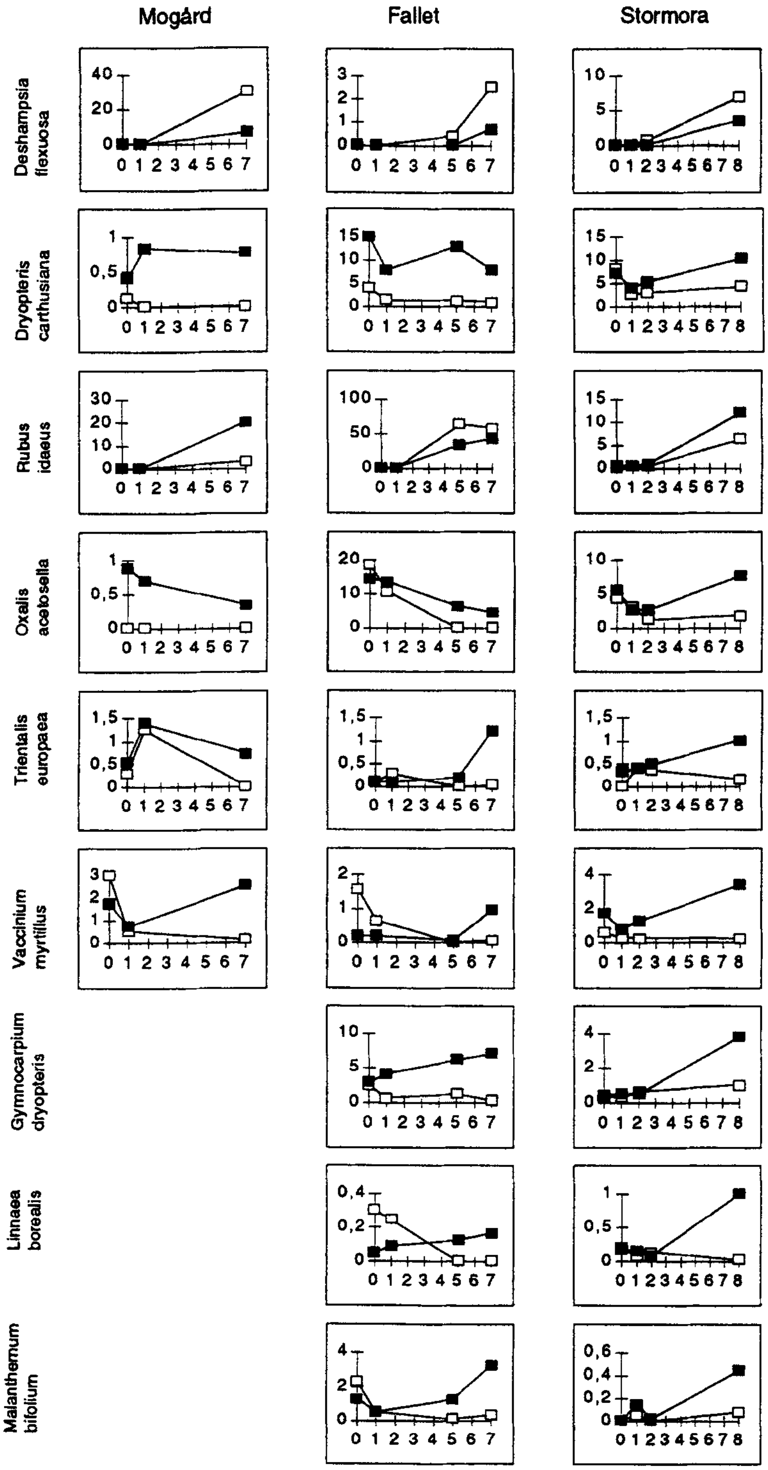

Fig. 6. Cover of selected species over the years after harvesting. The X-axis shows years after harvesting. Year 0 is the year before harvesting. The Y-axis shows the cover (%). Observe the different scales on the y-axis. Open squares = clearcut, filled squares = shelterwood.

tion is also confirmed by the environmental variables, expressed as indicator values (Fig. 3).

Before treatment, the sites were arranged along a gradient from Fallet in the low and left to Mogård in the upper and right part of the ordination. After treatment, all plots were found below and to the right of these. Clearcut plots were more separated from the plots before treatments than shelterwood plots (Fig. 3). The indicator values in the ordination showed that clearcut plots were changed towards lighter, more nitrogen rich and less moist conditions than shelterwood plots.

The PCA for the plots at Mogård, indicated changes for both clearcut and shelterwood plots towards lighter conditions (Fig. 4). Shelterwood plots moved towards higher moisture values. In contrast to the other sites, nitrogen values were higher in the shelterwood. At Fallet, clearcut plots shifted towards more light- and nitrogen- demanding species. Shelterwood plots were also moved along the light and nitrogen gradient, but to a much smaller extent. The moisture gradient was important in the separation between the treatments. Also at Stormora all plots shifted along the light and nitrogen gradient, being most pronounced for clearcut plots.

3.4. Responses of individual species

Altogether 101 vascular plant species were recorded in the subplots in all years. The number of species was naturally influenced by the number of subplots and sampling occasions. Fallet was the most species-rich site (78 recorded species), followed by Stormora (46), Mogård (27) and Labbaliden (23). Most species occured in low frequencies, and comparisons between species were restricted to the most common ones. Only 10 species occurred in all four sites, 23 in at least three sites, and 40 in at least two sites.

The most pronounced changes were observed at Fallet, where many of the dominant species before cutting were reduced in the clearcut, while they increased or remained the same in the shelterwood (Figs. 5 and 6, see also Appendix A). *R. idaeus* and other pioneer species such as *Cirsium arvense, Epilobium angustifolium* and *Filipendula ulmaria* increased considerably in the clearcut, with a total cover of 77% seven years after cutting. *O. acetosella* decreased dramatically in cover in the clearcut, from more than 18% to less than 1%. Other decreasing species were *Gymnocarpium dryopteris, L. muralis, M. bifolium, P. quadrifolia* and *V. myrtillus*. All these species increased or retained their cover in the shelterwood. A few other species that were present before harvesting increased their cover in the clearcut, e.g. *Fragaria vesca, Rubus saxatilis* and *Viola riviniana*.

The differences between clearcut and shelterwood were smaller at Mogård and Stormora. At Mogård the vegetation in the clearcut became dominated by

Table 5
Average indicator values (Ellenberg et al., 1991) for vascular plant species at all sites 7–8 years after harvesting, and results from Tukey's test

Site	Light		Moisture		pH		Nitrogen	
	Clearcut	Shelt.w.	Clearcut	Shelt.w.	Clearcut	Shelt.w.	Clearcut	Shelt.w.
Mogård	6.60	6.31	5.37	5.51	2.08	2.61	3.59	4.03
Labbaliden	6.69	5.62	5.18	5.54	3.18	2.88	5.66	4.65
Fallet	6.39	4.61	5.23	5.92	4.84	4.42	5.97	4.78
Stormora	5.34	5.04	6.52	6.48	3.90	3.56	4.16	3.74
Average, all sites	6.25	5.40	5.57	5.86	3.50	3.37	4.85	4.30
Tukey's test [a]		ns		ns		ns		ns

[a] Tukey's test of differences between treatments (model 1). Significance level: ns = not significant, [b] = $P < 0.05$, [c] = $P < 0.01$, [d] = $P < 0.001$.

Deschampsia flexuosa and tall sedges (*Carex* spp.). *R. idaeus* was more frequent and had higher cover in the shelterwood than in the clearcut, mainly because of frost-killing of the raspberry plants in the clearcut. Three relatively common species before harvesting, *D. carthusiana*, *T. europaea* and *V. myrtillus*, were greatly reduced in the clearcut, but increased in the shelterwood. In Stormora most species increased their cover after harvesting, both in the shelterwood and in the clearcut. This might partly be due to the late inventory date before harvesting compared with the inventory after 8 years (see Table 3). The relative change between shelterwood and clearcut was compared, and a few species were found to be disfavoured by the clearcut, e.g. *D. carthusiana*, *E. sylvaticum*, *O. acetosella* and *V. myrtillus*.

In Labbaliden (only analysed 7 years after treatment) the difference between the treatments was large. Some species that were common or rather common in the shelterwood were absent or rare in the clearcut, e.g. *Carex canescens*, *D. carthusiana*, *O. acetosella*, *T. europaea* and *V. myrtillus* (see Appendix A). The covers of *D. flexuosa*, *Galeopsis bifida* and *R. idaeus* were greater in the clearcut than in the shelterwood.

The negative effect of the clearcut, with respect to species representative of the old forest before harvesting, was evident for *D. carthusiana*, *O. acetosella*, *T. europaea* and *V. myrtillus* (Fig. 6) but, according to model 1, was significant only for *T. europaea* ($P < 0.01$). These species increased or almost retained their cover in the shelterwood. *G. dryopteris*, *Linnaea borealis* and *M. bifolium* showed the same pattern at Fallet and Stormora, whereas they were absent at Mogård.

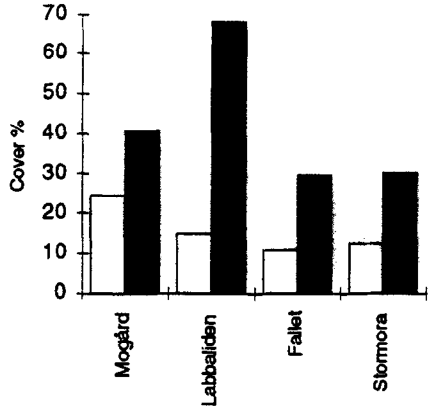

Fig. 7. Cover of all bryophytes in years 7–8 after harvesting. Open bars = clearcut, filled bars = shelterwood.

3.5. Indicator values

3.5.1. Light

Seven to eight years after cutting, the mean indicator value for light was higher in the clearcut than

Table 6
Total cover of vascular plant species indicating shaded, moist and nitrogen rich conditions at all sites 7–8 years after harvesting, and results from Tukey's test

Site	Shade [a]		Moist [b]		Nitrogen [c]	
	Clearcut	Shelt.w.	Clearcut	Shelt.w.	Clearcut	Shelt.w.
Mogård	0	0.4	6.7	7.8	3.4	20.5
Labbaliden	0	2.0	0.6	4.3	28.0	17.3
Fallet	0.7	35.3	8.3	36.1	72.3	48.3
Stormora	4.4	21.7	47.8	54.2	10.7	15.4
Average, all sites	1.3	14.8	15.9	25.6	28.6	25.4
Tukey's test [d]		ns		ns		ns

[a] Cover of species with indicator value for light 3 and lower.

[b] Cover of species with indicator value for moisture 7 and higher.

[c] Cover of species with indicator value for nitrogen 7 and higher.

[d] Tukey's test of differences between treatments (model 1). Significance level: ns = not significant, [e] = $P < 0.05$, [f] = $P < 0.01$, [g] = $P < 0.001$.

in the shelterwood at all sites (Table 5). One main portion of the difference is the absence of species preferring shaded conditions in the clearcut, e.g. *G. dryopteris*, *M. bifolium* and *O. acetosella* (Table 6). Compared with before cutting, the flora was converted into a more light-tolerant composition at all sites and treatments, but the change was most marked in the clearcut (Fig. 4).

3.5.2. Moisture

At Fallet, Mogård and Labbaliden the mean indicator value for moisture after harvesting was somewhat higher in the shelterwood than in the clearcut (Table 5), and in Stormora the value was about the same. The cover of species preferring moist or wet habitats, e.g. *E. sylvaticum*, was greater in the shelterwood at all sites (Table 6).

3.5.3. pH

At Fallet, Labbaliden and Stormora the indicator value for pH was higher in the clearcut than in the shelterwood (Table 5). No clear differences between

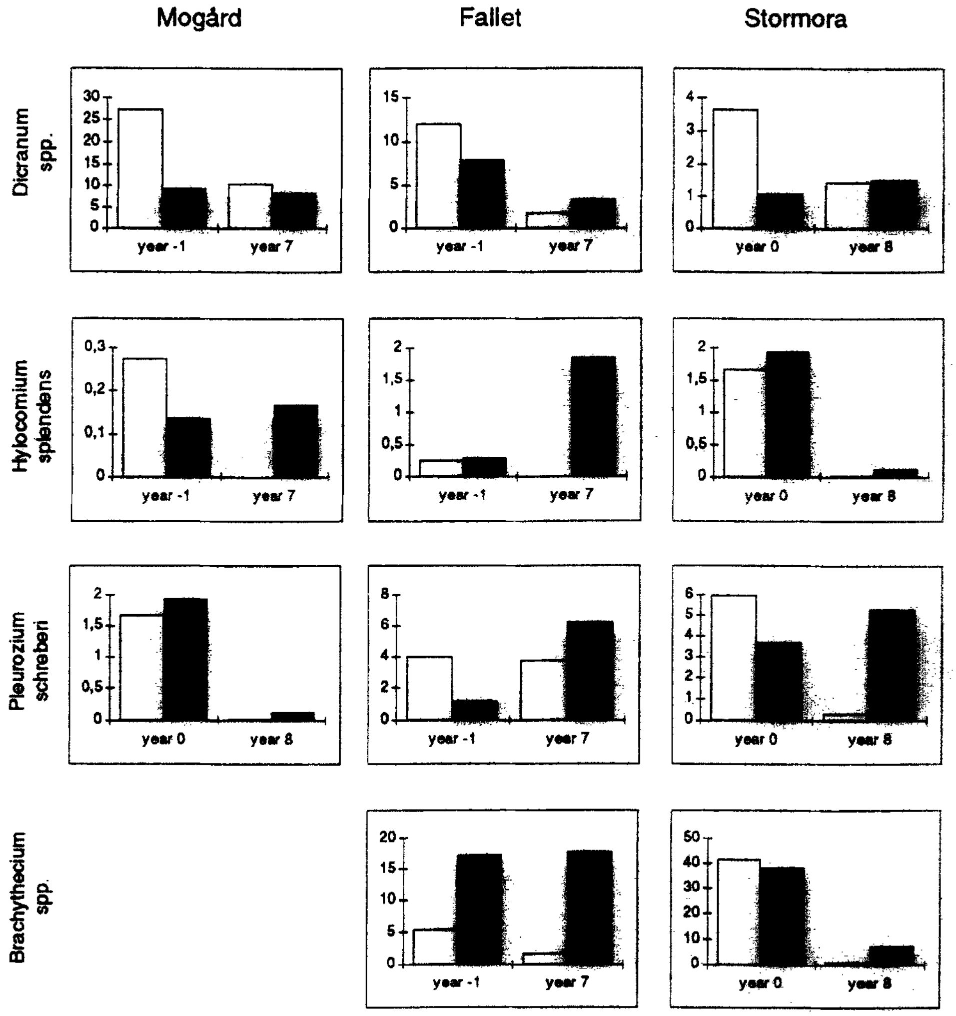

Fig. 8. Cover of bryophyte species and genera (%, y-axis) before (year 1 or 0) and after (year 7 or 8) harvesting. Observe the different scales on the y-axis. Open bars = clearcut, filled bars = shelterwood.

treatments were found when species preferring acid and basic conditions were regarded specifically.

3.5.4. Nitrogen availability

The mean indicator value for nitrogen availability was higher in the clearcut than in the shelterwood at all sites except Mogård (Table 5). The most pronounced differences were found at Fallet and Labbaliden. The result was explained both by species with low nitrogen demands (value 3 and lower) that were favoured in the shelterwood, and by species with high nitrogen demands (value 7 and higher) that were favoured in the clearcut (Table 6).

3.6. Changes in the bryophyte flora

The cover of bryophytes was lower in the clearcut than in the shelterwoods at all sites (Fig. 7). The difference was significant ($P < 0.05$) according to model 1. When compared with the cover before harvesting, bryophytes were greatly reduced in the clearcut at all sites: at Fallet from 29 to 11%; at Mogård from 60 to 25% and at Stormora from 76 to 12%. In the shelterwoods the cover was somewhat reduced at Fallet and Stormora, but increased (from an originally low level) at Mogård.

Many of the most common mosses in this forest type (*Brachythecium* spp. , *Dicranum* spp. , *Hylocomium splendens* and *P. schreberi*) were largely reduced in the clearcut (Fig. 8), and this was even more pronounced among more moist-demanding bryophytes such as *Plagiochila* spp. and *Mnium* spp. (not shown). With a few exceptions, these species retained or increased their cover in the shelterwood. Also *Sphagnum* species (mainly *S. girgensohnii*) were favoured by the shelterwood.

4. Discussion

4.1. Vegetation cover and height

The cover of the field vegetation increased considerably after cutting at all sites, which probably may be attributed mainly to the amount of released nutrients and reduced competition from the overstory biomass (Gholz et al., 1985). It had been assumed that ground cover as well as height of vegetation would be higher in the clearcut than in the shelterwoods, which was also found to be the case at Fallet after five years (Hannerz and Hånell, 1993). However, after 7 years, the highest biomass was found in the shelterwoods. A plausible explanation is that the clearcuts were affected by frost and frost-heaving, but the shelterwoods were not. We observed frost damage on *R. idaeus* at Fallet, Labbaliden and Mogård at the year of the last inventory. Frost-heaving was also obvious in the clearcut at all sites.

4.2. Diversity

Diversity was favoured by the shelterwood regime. Diversity increased in the shelterwood plots and was higher than in the clearcut at all sites, despite the observations from the last inventory being made in smaller subplots. In the clearcut, diversity decreased during the first one–two years after harvesting and then either increased (Mogård), remained unchanged (Stormora), or decreased (Fallet). The decrease at Fallet was the result of a few pioneers becoming dominant in the clearcut, mainly *C. arvense*, *F. ulmaria* and *R. idaeus*. *F. ulmaria* and *R. ideaus* increased in the shelterwood as well, but many of the late successional species also retained or increased their cover in this treatment, which led to a total increase in species-richness as well as in diversity. A drop in diversity immediately after disturbance was also reported by Schoonmaker and McKee (1988) in *Tsuga-Pseudotsuga* stands in North America. After this initial drop, the diversity increased with a peak occuring 15 years after clearcutting, before decreasing again. This trend, with the highest value of diversity in mid-succession in forests, has been reported by many authors (references in Huston, 1994).

A shelterwood cutting may be regarded as an "intermediate rate of disturbance" (Huston, 1994), which may lead to increased or maintained diversity. Gove et al. (1992) compared diversity trends after strip-cutting and clearcutting, and strip-cutting had the highest diversity both one and ten years after harvesting. Disturbances that occur close to the highest point of diversity in a forest succession usually have the most positive effect on diversity (Huston, 1994).

4.3. Response to environmental factors

The indicator values, as used in this study, showed that clearcutting resulted in a greater change than shelterwood harvesting, when considering light, moisture and nitrogen availability. This is also in accordance with what is generally observed when measuring the actual parameters (see review in Hannerz and Gemmel, 1994). Light (Ottosson-Löfvenius, 1993) as well as accumulation of nutrients in the understory (Outcalt and White, 1981; Gholz et al., 1985) increases after clearcutting, which denotes an elevated amount of available nitrogen. Kirby (1990) also found a shift towards light- and nutrient-demanding species after felling in broad-leaved forests in England, and also a shift towards more moisture-demanding species. The ground water table usually rises after cutting (Lundin, 1979), but the top layer might become temporarily dried-out (Braathe, 1956), and transpiration rates may increase (Huston, 1994). Individual species with their optimum in wet or semiwet habitats may therefore suffer from drought when exposed to clearcutting, but the opposite effect is also possible. According to Huston (1994) (his table 7.1), the most prominent feature of late successional species is their tolerance to shade and their reduced tolerance to water stress. In contrast, early successional species can survive water stress better.

Estimates of an environmental factor from indicator values can be computed as mean values from either presence/absence (p/a) values or cover/abundance (c/a) values. In this study, p/a values were used. According to Diekmann (1995), most authors reason that cover of species not only depends on environmental conditions, but also on their specific growth form. Thus p/a values are normally recommended. Diekmann (1995) and van Dobben (1993) compared the methods used under Swedish conditions. Diekmann (1995) found better fitness between indicator values for reaction and pH measured in soil when the indicator values were based on p/a values. When analysing fertilization, liming and acidification experiments, van Dobben (1993) found that p/a values corresponded best to the hypothesized effects of the treatments on vegetation. In this study, c/a values in some cases showed a greater difference between treatments than p/a values (results not shown), which could be explained by the massive expansion of a few species in the clearcut, e.g. *R. idaeus*, which was evened out when using p/a values.

Several species in this study lacked indicator values according to Ellenberg et al. (1991), hence new indicator values were constructed (see Appendix B). These were based mainly on ecological literature for Nordic conditions (Sjörs, 1956). In some cases, the original values were also changed. The original values were derived for Central European conditions, and Ellenberg et al. (1991) emphasized that they might not be applicable outside this area. Ellenberg numbers have, however, proved to be reasonable predictors outside Central Europe, e.g. in Great Britain (Thompson et al., 1993). Attempts have been made to calibrate the values for Swedish conditions. Diekmann (1995) improved values experimentally for a number of species in deciduous forests in Central Sweden. Adjustments were made for 16 vascular plant species in a study by Gustafsson (1994). Values suggested by Diekmann (1995) and Gustafsson (1994) were used in this study.

4.4. Bryophytes

The moss flora was largely affected by the clearcutting at all sites, and dominant mosses, e.g. *Brachythecium* spp. , *H. splendens* and *P. schreberi* were to some extent replaced by early successional species such as *Polytrichum* spp. and *Pohlia nutans* (data not shown). To our knowledge, no studies have been made of the effects on bryophytes of clearcutting in boreal forests. Schimmel (1993) studied succession of mosses following fire disturbance. He found that acrocarpous mosses, e.g. *Ceratodon purpureus* and *Polytrichum* spp. dominated during the first 20–30 years, but were thereafter outcompeted by pleurocarpous mosses such as *H. splendens* and *P. schreberi*. Recolonization of pleurocarpous mosses occurred 5–15 years earlier if a tree canopy survived the fire (Schimmel, 1993). Heavy recolonization of forest mosses, mainly *Hylocomium* and *Rhytidiadelphus* occurred at 50–70 years after understory removal in conifer forest of south-east Alaska (Alaback, 1982).

4.5. Implications for forestry practises and conservation

From a conservation point of view one must be aware that the sites in this study are not representative of natural wet forests, as they have been drained and managed with silvicultural measures. However, species characteristic to such forests, with shaded and wet or moist habitats, were also common in the sites we studied. Berg et al. (1994) reported that shaded habitats were important for 28% of all threatened species in the Swedish red-list, and were especially important for cryptogams. In contrast, most vascular plants (77%) on the red-list preferred semi-shaded or sun-exposed habitats. Moist and wet conditions were important for a minor part (8.5%) of all the red-list species. The main factor for preserving redlist species in natural wet forests seemed to be the occurrence of dead wood (Berg et al., 1994), which is reduced in a managed forest.

None the less, the shelterwood system offers a harvesting regime that is less destructive to the forest flora than the clearcutting system. Selection and shelterwood systems are also suggested as silvicultural practices that maintain stability in ecosystems, and possibly control of the biogeochemical cycle (Larsen, 1995). The advantages for the flora are probably most pronounced for late successional species in moist or wet habitats. These habitats often coincide with sites where forest regeneration after clearcutting is difficult. On fertile peatlands, mortality of the planting stock from frost, competing vegetation, water-logging and pine weevils may be severe after clearcutting. A shelterwood reduces these injurious factors to a large extent (Hånell, 1993; Hannerz and Gemmel, 1994; von Sydow and Örlander, 1994). Hence, conflicts between forestry and conservation will be reduced.

Our study was carried out in uniform shelterwoods. There are also other types of shelterwoods that might further reduce conflicts between conservation and forestry interests. For example, in the irregular shelterwood system some shelter trees are maintained over a long and indefinite regeneration period, which results in an uneven-aged forest (Matthews, 1989).

As succession proceeds after harvesting, the differences between clearcutting and shelterwood cutting may be evened out as the new overstory develops. For a few species though, the critical period immediately after clearcutting may be the determining factor for their survival. When the shelter trees are harvested, in order to provide sufficient space for the developing regeneration, a new disturbance is introduced. The effect of that disturbance on the flora is probably smaller, but remains to be studied.

4.6. Conclusions

The results of this study indicate that a shelterwood system has advantages in preserving the late successional flora in spruce stands on fertile peatlands, compared with the clearcutting system. The positive effects were most pronounced at the most fertile and species-rich site. Shelterwood harvesting was found especially to favour vascular plants that prefer shaded and moist conditions.

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Appendix A

Frequency (% of subplots) and mean cover of vascular plants before and 7–8 years after cutting at the different sites. t = trace (cover less than 0.01%).

Only species present in at least two subplots at any site are shown. The total number of registered species on all occasions are given for each site. (See Tables 7–10.)

Table 7
Fallet

	Frequency				Cover			
Year after cutting	0	0	7	7	0	0	7	
Treatment	clearc	sheltw	clearc	sheltw	clearc	sheltw	clearc	sheltw
No. of subplots	42	60	40	90	42	60	40	90
Agrostis capillaris / canina	0	2	8	6	0	t	0.5	0.37
Anemone nemorosa	29	20	0	1	0.12	0.08	0	0.03
Anthriscus sylvestris	0	2	0	4	0	0.03	0	0.13
Athyrium filix-femina	0	2	0	1	0	0.12	0	0.67
Calamagrostis arundinacea	0	0	8	6	0	0	1.12	0.77
Calamagrostis canescensens	0	8	0	0	0	0.05	0	0
Carex canescens / brunnescens	0	0	8	0	0	0	0.2	0
Carex digitata	60	38	3	14	0.31	0.19	0.12	0.67
Carex vaginata	2	0	0	2	t	0	0	0.08
Chrysosplenium alternifolium	0	5	0	1	0	0.01	0	0.01
Cirsium arvense	0	0	53	0	0	0	4.1	0
Cirsium vulgare	0	0	13	0	0	0	0.32	0
Deschampsia flexuosa	5	0	23	6	t	0	2.54	0.69
Cryopteris carthusiana	69	90	10	47	3.99	14.99	1.04	8.12
Elymus caninus	0	0	3	2	0	0	0.25	0.08
Epilobium angustifolium	0	5	83	17	0	0.01	8.50	0.81
Equisetum pratense	0	33	0	27	0	0.43	0	0.92
Equisetum sylvaticum	0	43	0	80	0	0.61	0	15.96
Filipendula ulmaria	12	23	20	22	0.05	0.26	5.55	7.73
Fragaria vesca	2	20	13	21	0.01	0.18	2.25	0.47
Galeopsis bifida	0	0	20	4	0	0	0.30	0.03
Galium palustre	0	0	0	2	0	0	0	0.01
Geum rivale	0	8	3	4	0	0.18	0.3	0.16
Gymnocarpium dryopteris	14	42	8	32	2.45	2.85	0.28	7.08
Hepatica nobilis	19	3	3	3	0.22	0.07	0.02	0.19
Lactuca muralis	38	10	0	8	0.32	0.09	0	0.13
Linnaea borealis	45	17	0	3	0.30	0.05	0	0.17
Luzula pilosa	31	37	0	28	0.09	0.07	0	0.93
Lycopodium annotinum	17	0	0	1	0.43	0	0	0.03
Maianthemum bifolium	86	72	20	60	2.29	1.31	0.36	3.26
Melampyrum sylvaticum	5	0	3	3	0.01	0	0.1	0.09
Melica nutans	0	0	5	6	0	0	0.18	0.22
Milium effusum	0	5	3	17	0	0.09	0.25	0.82
Moehringia trinervia	0	0	3	4	0	0	0.02	0.09
Oxalis acetosella	100	100	5	76	18.52	14.55	0.04	4.51
Paris quadrifolia	31	42	0	22	0.34	0.62	0	0.93
Poa palustris	0	0	0	7	0	0	0	0.33
Potentilla erecta	2	0	5	0	0.01	0	0.28	0
Ranunculus repens	0	3	0	2	0	0.02	0	0.06
Rubus idaeus	17	38	100	94	0.61	1.30	58.55	44.02
Rubus saxatilis	69	23	35	11	1.33	0.57	1.42	0.93
Rumex acetosa	0	0	5	1	0	0	0.28	t
Rumex acetosella	0	0	10	0	0	0	0.24	0
Silene dioica	0	7	5	9	0	0.15	0.11	0.68
Solidago virgaurea	19	0	23	6	0.32	0	1.25	0.21
Stellaria longifolia	0	8	8	18	0	t	0.09	0.34
Taraxacum vulgare	0	0	8	0	0	0	0.18	0
Thelypteris phegopteris	0	18	0	18	0	0.65	0	2.84
Trientalis europaea	24	17	8	52	0.11	0.12	0.04	1.23

Table 7 (continued)

	Frequency				Cover			
Year after cutting	0	0	7	7	0	0	7	
Treatment	clearc	sheltw	clearc	sheltw	clearc	sheltw	clearc	sheltw
No. of subplots	42	60	40	90	42	60	40	90
Urtica dioica	0	3	10	19	0	0.07	0.27	1.25
Vaccinium myrtillus	60	15	5	10	1.59	0.20	0.08	0.94
Vaccinium vitis-idaea	24	3	5	0	0.18	0.01	0.05	0
Veronica chamaedrys	0	0	0	7	0	0	0	0.4
Veronica officinalis	0	2	0	2	0	0.02	0	0.02
Viola epipsila	0	28	0	28	0	0.37	0	4.26
Viola palustris	5	2	3	4	0.03	0.02	0.1	1.52
Viola riviniana	40	25	35	16	0.73	0.20	4.05	0.32

Total number of species on all occasions and in all subplots: 78.

Table 8
Mogård

	Frequency				Cover			
Year after cutting	0	0	7	7	0	0	7	7
Treatment	clearc	sheltw	clearc	sheltw	clearc	sheltw	clearc	sheltw
No. of subplots	54	56	60	120	54	56	60	120
Calamagrostis canescens	0	2	0	1	0	t	0	0.05
Calluna vulgaris	2	2	42	27	t	0.05	6.3	8
Carex cespitosa	0	0	3	0	0	0	0.5	0
Carex canescens / brunnescens	2	0	13	21	t	0	3.08	4.53
Carex echinata	2	0	5	13	t	0	1.01	1.35
Carex nigra	0	0	0	2	0	0	0	0.32
Carex sp.	0	0	15	0	0	0	6.06	0
Deschampsia cespitosa	0	0	2	3	0	0	0.42	0.46
Deschampsia flexuosa	9	4	83	49	0.02	0.09	30.33	6.77
Dryopteris carthusiana	4	23	2	13	0.13	0.41	0.02	0.78
Epilobium angustifolium	0	0	0	10	0	0	0	0.20
Eriophorum vaginatum	0	0	3	2	0	0	0.48	0.17
Juncus conglomeratus	0	0	0	2	0	0	0	0.24
Juncus effusus	0	0	8	7	0	0	1.1	0.33
Lycopodium annotinum	4	2	0	0	0.09	t	0	0
Molinia caerulea	0	0	2	2	0	0	0.13	0.02
Oxalis acetosella	0	18	0	3	0	0.88	0	0.35
Potentilla erecta	0	0	2	3	0	0	0.05	0.03
Rubus idaeus	0	4	45	71	0	0.04	3.31	20.33
Rumex acetosella	0	0	2	1	0	0	t	t
Senecio spp.	0	0	5	6	0	0	0.05	0.02
Trientalis europaea	30	18	3	25	0.31	0.56	0.02	0.74
Vaccinium myrtillus	83	71	17	45	2.97	1.75	0.16	2.55
Vaccinium vitis-idaea	44	34	12	27	0.46	0.28	0.48	2.32

Total number of species on all occasions and in all subplots: 27.

Table 9
Stormora

	Frequency				Cover			
Year after cutting	0	0	8	8	0	0	8	8
Treatment	clearc	sheltw	clearc	sheltw	clearc	sheltw	clearc	sheltw
No. of subplots	24	16	80	160	24	16	80	160
Calamagrostis purpurea	58	13	58	44	0.30	0.02	7.69	12.66
Carex brunnescens	46	13	29	23	0.14	t	2.74	1.72
Carex globularis	25	50	36	70	0.02	2.26	13.79	14.44
Cornus suecica	0	6	0	3	0	t	0	0.08
Deschampsia cespitosa	0	0	45	12	0	0	14.64	2.49
Deschampsia flexuosa	13	0	36	23	0.07	0	6.86	3.53
Dryopteris carthusiana	83	81	53	49	8.34	7.14	4.27	10.4
Epilobium angustifolium	0	0	70	53	0	0	4.34	3.04
Epilobium palustre	0	0	0	2	0	0	0	0.05
Equisetum pratense	0	0	1	1	0	0	t	0.01
Equisetum sylvaticum	100	88	64	62	1.94	2.59	1.44	9.60
Gymnocarpium dryopteris	38	13	20	28	0.38	0.44	1.03	3.83
Lactuca alpina	0	0	0	1	0	0	0	0.08
Linnaea borealis	17	19	4	13	0.18	0.19	0.02	0.99
Luzula pilosa	4	6	0	4	t	t	0	0.16
Lycopodium annotinum	0	0	0	3	0	0	0	0.09
Maianthemum bifolium	4	0	11	16	t	0	0.08	0.44
Orthilia secunda	0	19	0	0	0	0.10	0	0
Oxalis acetosella	96	88	65	74	4.46	5.47	1.88	7.69
Poa sp.	0	0	4	1	0	0	0.18	0.02
Rubus arcticus	0	0	15	12	0	0	3.44	3.81
Rubus chamaemorus	0	0	0	8	0	0	0	1.11
Rubus idaeus	17	6	33	36	0.35	0.12	6.36	12.02
Rumex acetosa	0	0	10	0	0	0	0.54	0
Rumex acetosella	0	0	3	0	0	0	0.07	0
Stellaria longifolia	8	6	11	11	t	t	0.90	0.18
Trientalis europaea	25	50	29	49	0.03	0.33	0.16	1.02
Vaccinium myrtillus	42	56	9	31	0.62	1.71	0.26	3.41
Vaccinium vitis-idaea	17	38	4	26	0.04	0.39	0.13	2.68
Veronica officinalis	0	0	1	0	0	0	0.01	0
Viola palustris	4	6	10	8	0.08	0.12	0.89	0.29

Total number of species on all occasions and in all subplots: 46.

Table 10
Labbaliden

	Frequency		Cover	
Year after cutting	7	7	7	7
Treatment	clearc	sheltw	clearc	sheltw
No. of subplots	60	119	60	119
Agrostis capillaris	5	2	0.07	0.04
Carex canescens / brunnescens	10	17	0.35	2.63
Carex echinata	2	1	0.02	0.03
Deschampsia flexusa	45	27	5.55	2.56
Dryopteris carthusiana	3	18	0.05	0.98
Epilobium angustifolium	10	7	0.24	0.32
Equisetum sylvaticum	0	8	0	0.34
Galeopsis bifida	12	3	0.53	0.01
Galium uliginosum	3	4	0.06	0.24
Juncus conglomeratus	3	0	0.18	0
Lycopodium annotinum	0	3	0	0.5
Maianthemum bifolium	0	5	0	0.16
Moehringia trinervia	3	0	0.02	0
Oxalis acetosella	0	20	0	1.00
Rubus idaeus	73	64	27.68	17.01
Rumex acetosa	7	0	0.48	0
Senecio spp.	7	1	0.06	t
Trientalis europaea	0	21	0	0.86
Vaccinium myrtillus	5	57	0.04	8.62
Vaccinium vitis-idaea	5	8	0.18	0.20
Viola palustris	0	3	0	0.05

Total number of species in all subplots: 23.

Appendix B

Indicator values from Ellenberg et al. (1991) that were adjusted or constructed, based on Sjörs (1956), Gustafsson (1994) and Diekmann (1995). An initial value of 0 means that no indicator value was given in Ellenberg et al. (1991).

Light: *Carex digitata* from 3 to 5, *Carex globularis* from 0 to 6, *Luzula pilosa* from 2 to 6, *Rubus arcticus* from 0 to 7, *Rubus saxatilis* from 7 to 5, *Taraxacum vulgare* from 7 to 5.

Moisture: *Agrostis capillaris* from 0 to 4, *Alchemilla vulgaris* coll. from 0 to 6, *Carex globularis* from 0 to 8, *Deschampsia flexuosa* from 0 to 5, *Dryopteris carthusiana* from 0 to 5, *Lactuca muralis* fom 5 to 7, *Oxalis acetosella* from 5 to 7, *Rubus arcticus* from 0 to 7, *Rubus idaeus* from 0 to 5, *Vaccinium uliginosum* from 0 to 7.

pH-reaction: *Anthriscus sylvestris* from 0 to 7, *Carex digitata* from 0 to 6, *Carex globularis* from 0 to 2, *Convallaria majalis* from 0 to 5, *Equisetum sylvaticum* from 5 to 3, *Filipendula ulmaria* from 0 to 7, *Fragaria vesca* from 0 to 5, *Lactuca muralis* from 0 to 5, *Luzula pilosa* from 5 to 3, *Melica nutans* from 0 to 5, *Milium effusum* from 5 to 7, *Oxalis acetosella* from 4 to 6, *Veronica chamaedrys* from 0 to 5.

Nitrogen availability: *Alchemilla vulgaris* coll. from 0 to 6, *Carex globularis* from 0 to 2, *Luzula pilosa* from 4 to 3, *Rubus arcticus* from 0 to 3, *Rubus idaeus* from 6 to 8, *Solidago virgaurea* from 4 to 5, *Tussilago farfara* from 0 to 6, *Vaccinium uliginosum* from 3 to 2, *Viola riviniana* from 0 to 6.

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