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CHANGES IN THE COMMUNITY STRUCTURE OF FOREST FLOOR VEGETATION AFTER REPEATED LITTER DISTURBANCE BY RAKING

TAPIO LINDHOLM and MATTI NUMMELIN

Seloste

TOISTUVAN KARIKEHARAVOINNIN AIHEUTTAMAT MUUTOKSET METSIKÖN ALUSKASVILLISUUDESSA

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The tolerance of disturbance of the ground and field layer vegetation in a moderately fertile spruce stand (OMT) in southern Finland was studied. The study sites were the yard of a summer cottage and a virgin forest situated near by. The yard had been raked regularly during the last 25 years. The structure of the vegetation was quite different in these two originally similar areas. The phytomass and percentual coverage of the vegetation was remarkable lower in the raked habitat. Tall mosses, *Pleurozium schreberi* and *Hylocomium splendens* had especially disappeared. Most grass species had also deteriorated. Only *Deschampsia flexuosa* was quite tolerant to raking. The phytomass of the dwarf shrubs was lower in the raked area but their relative productivity was higher. Three different kinds strategies of species was described: species of virgin shaded forest, species of meadow-like forest floor and species which tolerate or benefit from the disturbance. The raked habitat had a higher species diversity than the virgin area. Nitrogen and carbon contents were lower in the soil of the raked area.

INTRODUCTION

The dominant feature of vegetation in mature coniferous forests, is the stability of the species composition and the structure of the floor vegetation (e.g. Linkola 1916). The classification of forest vegetation by the traditional Cajander theory (e.g. Cajander 1909, Frey 1973) is based on the relative stability of climax forest floor vegetation in different areas. However, the disturbance of vegetation induces changes in the structure of vegetation. Theoretical interest in the composition changes is based on the relationship between the environmental load and the productivity of a plant community and the diversity of the community (e.g. Huston 1979).

Outdoor recreational activities are often concentrated in virgin forest areas. Problems have, however, arisen, when natural areas are subjected to trampling, camping, the passage of vehicles or the use of summer cottages, which is so intensive that the original vegetation is destroyed by these recreational activities. This is a matter of great interest and practical value. In 1976 there were a total of 230 000 summer cottages in Finland (Arovaara et al. 1980) and spending some time at a summer cottage is the most popular form of recreation in nature.

The aim of this study was to analyse and describe the patterns of change in the community structure of floor vegetation in fertile coniferous stands after permanent disturbance.

The raking of forest vegetation was chosen as the study object because this simple manipulation of a plant community offered an ideal opportunity to study some aspects of plant communities of forest ecosystem. This work is also a contribution to studies on the effect of human activities on natural ecosystems (e.g. Liddle 1975, Kellomäki 1977).

We are indebted to the parents and aunt of MN for providing "the experiment" for our use. Timo Kairesalo helped us with the C and N analyses at the Institute of Limnology, University of Helsinki. Seppo Kellomäki and Lauri Oksanen made valuable comments on the draft.

STUDY AREA

The study sites were situated near Vammala (23°06'E, 61°25'N) in south-western Finland. The area belongs to the southern boreal forest vegetation zone (Ahti et al. 1968). Rich forest types are rather common in the study area (Mäkelä 1936, Suominen 1961).

The vegetation in the study site was quite rich, mostly resembling the *Oxalis acetosella – Vaccinium myrtillus* site type (OMT). The summer cottage and forest were lying near to a lake, the ground sloping about 0.5 m between the study plots (Fig. 1). Two separate sites were chosen for detailed study. One represented an area which has been the yard of a summer cottage for a long time and the other a forest habitat where no silvicultural treatment has been carried out for over 30 years.

Originally, there were no significant differences between these two sites because they are both part of the same homogenous forest. The only difference has followed from the summer cottage and the human activities taking place around it. The activity introduced by man which has had the greatest disturbing effect on the vegetation has been the raking away of the litter in the yard every autumn during the past 25 years. Trampling is not great on the studied site because paths have been laid out for walking.

The raking has been performed each autumn so intensively that all the litter and loose plant material – L horizon (Erlich et al. 1974) – has been removed from the area. The humus layer – F and H horizons – has also disappeared over the course of time and only the H horizon has remained up to now.

The light reaching the floor vegetation is significantly regulated by the structure of the tree layer as demonstrated by e.g. Monsi & Saeki (1953). However, in this case the distribution of the trees on both sites is so uneven that unshaded areas can be found in the natural forest and there is quite a lot of shade under the trees in the yard, too.

The factor which mainly affects the vegetation structure of a raked habitat is a complex stress factor, in which the effect of litter removal is only one part.

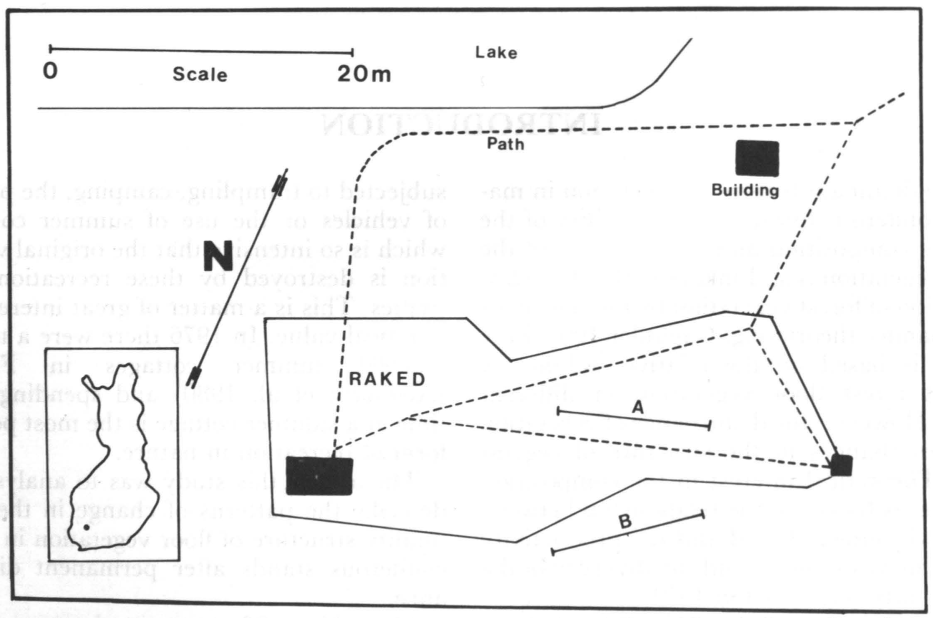

Fig. 1. Lay-out of the study area. The raked yard area is dotted. Dotted lines indicate the paths. Lines A and B show the places where the lines for study plots were situated. A is the virgin forest floor study area and B is the raked forest floor study area.

MATERIAL AND METHODS

Samples were taken in late August, 1979, when the biomass was considered to be at its maximum. The percentage coverage of the plants was determined from ten 1×1 m sampling plots in both areas. The sample plots were laid out systematically along a line, one metre apart from each other. The following percentages were used in coverage analysis: 0, trace (+), 1, 2, 3, 5, 7, 10, 15, 20, 30, 40, 50, 60, 70, 80, 86, 90, 95, 97, 98, 99, and 100. The line was drawn randomly through the centre of the raked area and randomly through the unraked forest in the immediate vicinity of the yard.

All field and ground layer vegetation and undecomposed litter was cut off at the soil surface over an area 25×25 cm in the centre of each analyzed 1×1 m sample plot. The harvested material was then sorted into species separately for each sample and the current growing season's shoot increment of dwarf shrubs and other plants with perennial shoots was separated from the older phytomass. The annual length increment of each shoot was considered to represent the annual above-ground production. The phytomass of the annual shoots of grasses at the moment of harvesting was considered to represent the annual above-ground production of these species. The annual production of mosses and lichens was not estimated. Only total phytomass values for each species are presented here.

The fractions were packed into separate paper bags, dried at 65°C for appr. 48 hours and weighed (Gimingham & Miller 1968) to an accuracy of 0.01 g.

The soil samples for the carbon and nitrogen analyses were taken from the centre of every third sample plot along the sampling line. The samples were taken from the upper zone (ca. 5 cm) of the Ah-horizon (Erlich et al. 1974) of the podsol soil. Before the analyses about 100 g of each sample was homogenized. After that, the samples were combined into two collective samples, for virgin and for raked soils respectively. The analyses were carried out on a Hewlett-Packard CHN-analyzer.

In the calculations the following formulae were used: Diversity index was calculated by the Shannon-Wiener formula (e.g. Riclefs 1980):

$$H = -\sum_{i=1}^{N} P_i \log_e P_i, \qquad (1)$$

where H is the Shannon–Wiener diversity index, N is the number of species, P_i is the proportional amount of each species, and e is the base of Napierian logarithms.

Comparison of the similarity of different plant life forms in both habitats was analysed using the similarity index of Sørensen (1948):

$$qs = \frac{2c}{a + b}, \qquad (2)$$

where qs is the similarity index of Sørensen, a and b are the numbers of species in the virgin and raked sites, and c is the number of species which occur on both sites.

The scientific names of the vascular plants used in this study are according to Hämet-Ahti et al. (1981), and the scientific names of bryophytes are according to Koponen et al. (1977).

RESULTS

Species richness

The number of species is higher in the raked than in the virgin area (46–40, Fig. 2). The similarity of species composition in the different vegetation life forms in the raked and virgin areas is highest in the case of dwarf shrubs (7.71). The similarity index for the mosses is 5.43, and for the grasses 2.85.

The raked area has a significantly ($p < 0.1$) higher diversity index, calculated from the percentual coverages of the plants (Hutchinson 1973), in the total floor vegetation than in the virgin area (2.67–1.92, Fig. 3) This is mainly due to the large diversity differences in the ground layer (2.67–0.55). When the diversity is calculated on the basis of the dry weights of the species there are no statistical significant differences.

The differences in the diversities can also be seen in the relative abundance curves of the species (Fig. 4). The differences are clear in the curves for the percentual coverages of the plant species. The two most common species in the virgin area (both mosses, see also Table 1) have higher relative abundances than the most common species pair (grass-moss) in the raked area. Furthermore the slope of the curve is steeper in the case of the species of the virgin area (especially the common species) than in the curve for the species from raked area. The relative abundance curves of species based on the dry weights of the plants evidently do not differ from each other.

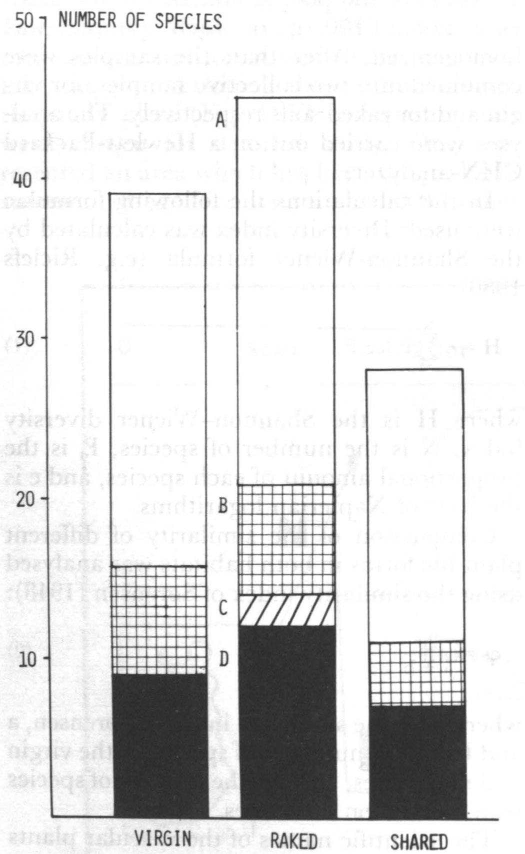

Fig. 2. The number of species in the virgin and raked areas, and the number of species which are present in both the virgin and raked areas (shared). A grasses, B dwarf shrubs, C lichens and D bryophytes.

Biomass

The biomass of the raked vegetation is only about one half that in the virgin forest floor (77–147 g/m^2, Fig. 5, Table 1). The difference is most evident in the dry weights of the grasses. The biomass of the grasses of the raked area is only about one seventh that in the virgin area (7–50 g/m^2). The biomass of the mosses and the dwarf shrubs is also smaller in the raked area, 76–55 and 21–14 g/m^2 respectively. However, the percentage productivity of dwarf shrubs is lower in the virgin than in the raked area. The raked area has less than one half amount of the litter in the virgin area (355–811 g/m^2).

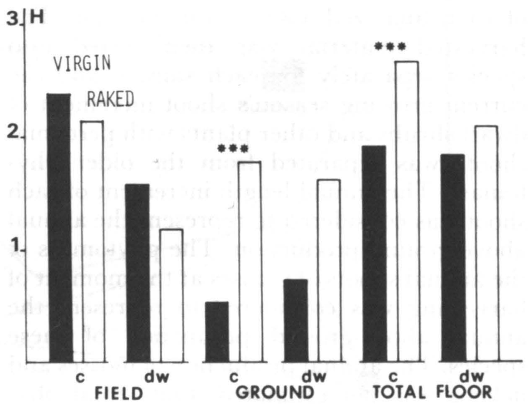

Fig. 3. Shannon-Wiener diversity indices (H) in the virgin and in the raked sample plots in the field and ground vegetation layers and in the total floor vegetation. Diversities are calculated both from the percentual coverages and the dry weights of the species. Asterisks indicate the difference in the level of $p < 0.001$ between the virgin and the raked area (t-test).

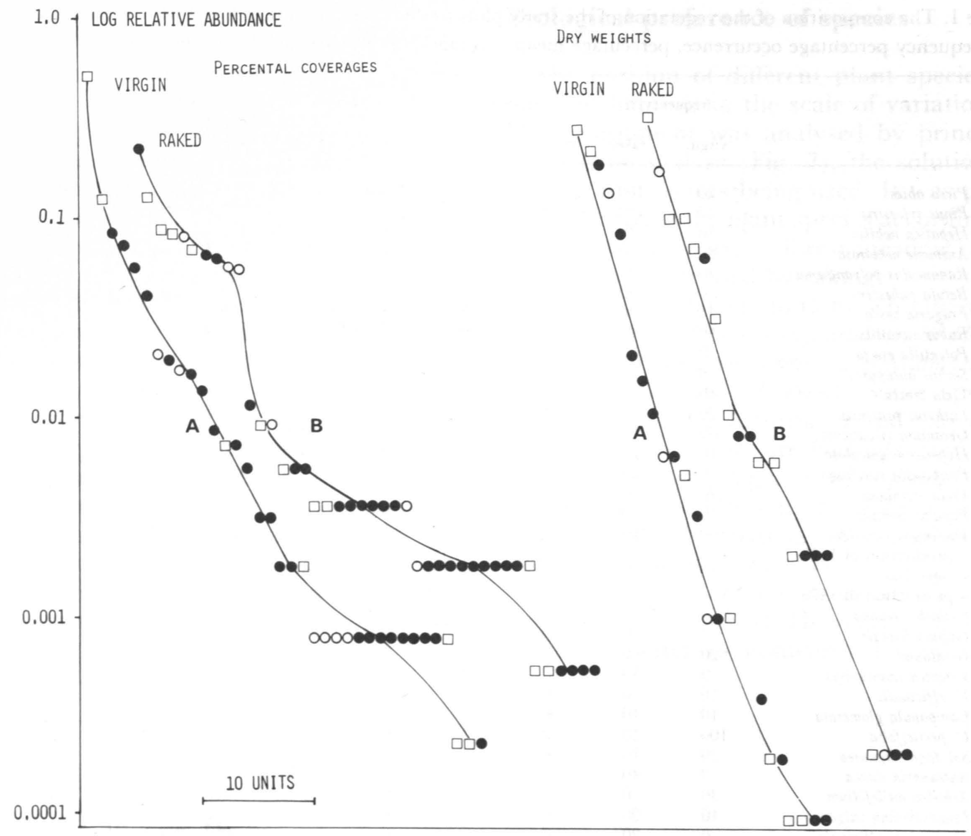

Fig. 4. Relative abundance curves of the plant species on the virgin and raked sample plots. The curves are drawn from the percentage coverages (curves on left) and the dry weights (curves on right) of the species. Symbols: circles for dwarf shrubs, dots for grasses and squares for bryophytes and lichens.

The mosses *Hylocomium splendens* and *Pleurozium schreberi* had the highest dry weights (47 and 36 g/m^2) out of the plants in the forest in the virgin forest. In the field layer of the virgin area, the highest dry weights were obtained for *Vaccinium vitis-idea* (34 g/m^2), *Deschampsia flexuosa* (23 g/m^2) and *Fragaria vesca* (16 g/m^2). In the raked area the moss *Brachytecium curtum* the highest dry weight (25 g/m^2). However, its biomass is only about one half that of the predominating moss in the virgin forest. In the raked forest, the next most common mosses – *Dicranum polysetum*, *Pohlia nutans* and *Hylocomium splendens* – had a dry weight of about 10 g/m^2. The only field layer species in the raked forest which had a dry weight of over 10 g/m^2 is *Vaccinium vitis-idea* (17). The mean dry weight of the moss species was 15 g/m^2 in the virgin forest and only one half of this value in the raked forest.

Table 1. The composition of the vegetation of the study plots in the virgin and raked forest floor areas performed by frequency percentage occurrence, percentage mean coverages and the dry weights of the species.

		frequency %		virgin cover		raked cover		virgin dry weight		raked dry weight	
		virgin	raked	mean %	+s.d.	mean %	+s.d.	g/m²	+s.d.	g/m²	+s.d.
18	*Picea abies*	20	100	+	–	0.5	0.5	0	0	0	0
19	*Pinus sylvestris*	20	100	+	–	+	–	0.2	–	0.2	0.0
21	*Hepatica nobilis*	10	10	+	–	+	–	0	0	0	0
22	*Anemone nemorosa*	80	0	2	2	0	0	0.3	–	0	0
25	*Ranunculus polyanthemus*	10	20	+	–	+	–	0	0	0	0
41	*Betula pubescens*	0	20	0	0	+	–	0	0	0.2	–
10	*Fragaria vesca*	40	80	3	4	4	9	16.5	0	1.9	2.8
6	*Rubus saxatilis*	40	90	3	6	3	3	4.8	0	0.2	0
46	*Potentilla erecta*	0	20	0	0	+	–	0	0	0.2	0
44	*Sorbus aucuparia*	0	20	0	0	+	–	0	0	0	0
23	*Vicia cracca*	10	0	+	–	0	0	0	0	0	0
24	*Lathyrus pratensis*	20	10	+	–	+	–	0.2	0	0	0
8	*Geranium sylvaticum*	60	60	5	7	0.5	0.5	7.7	5.4	1.9	–
14	*Hypericum maculata*	10	0	+	–	0	0	0	0	0	0
43	*Pimpinella saxifraga*	0	20	0	0	+	–	0	0	0	0
9	*Viola riviniana*	70	60	0.5	0.5	+	–	1.7	–	0	0
20	*Populus tremula*	10	0	+	–	0	0	0	0	0	0
4	*Vaccinium vitis-idea*	100	100	7	5	5	5	34.2	24.7	16.7	16.6
	– production of 1979							14.3	9.6	10.0	12.8
5	*V. myrtillus*	40	30	2	4	3	6	5.5	–	7.8	0
	– production of 1979							3.0	–	2.6	0
15	*Orthilla secunda*	20	0	+	–	0	0	2.2	0	0	0
11	*Galium boreale*	30	0	0.5	1	0	0	0.7	0.6	0	0
12	*G. album*	20	0	+	–	0	0	0	0	0	0
26	*Veronica chamaedrys*	0	10	0	0	+	–	0	0	0	0
50	*V. officinalis*	10	0	+	–	0	0	0	0	0	0
29	*Campanula glomerata*	10	10	+	–	+	–	0	0	0	0
7	*C. persicifolia*	100	40	2	2	+	–	3.4	4.0	0.2	–
28	*Solidago virgaurea*	10	10	+	–	+	–	0	0	0	0
48	*Antennaria dioica*	0	40	0	0	0.5	0.5	0	0		
16	*Achillea millefolium*	30	0	0.5	1	0	0	2.2	0	0	0
58	*Leucanthemun vulgare*	10	20	+	–	+	–	0.2	0	0	0
42	*Taraxacum officinale*	0	20	0	0	+	–	0	0	0.2	0
45	*Hieracium umbellatum*	0	50	0	0	0.5	2	0	0	0	0
17	*Convallaria majalis*	0	0	+	–	0	0	0	0	0	0
47	*Luzula pilosa*	90	20	1	1	+	–	9.6	0	3.5	0
2	*Carex digitata*	100	50	9	4	3	3	13.0	11.0	1.1	1.6
13	*Melica nutans*	2	10	1	3	+	–	0	0	0	0
40	*Poa nemoralis*	0	10	0	0	+	–	0	0	0	0
49	*Deschampsia cespitosa*	0	10	0	0	+	–	0	0	0	0
1	*D. flexuosa*	100	100	10	9	12	6	23.4	23.2	5.2	3.9
27	*Agrostis capillaris*	10	30	+	–	+	–	0	0	0.6	0.5
54	*Barbilophozia barbata*	0	80	0	0	+	–	0	0	4.3	5.8
56	*Ptilidium ciliare*	0	10	0	0	+	–	0	0	0.2	0
59	*Atrichum undulatum*	10	0	+	–	0	0	0	0	0	0
60	*Dicranum majus*	0	10	0	0	+	–	0	0	0	0
33	*Dicranum polysetum*	40	60	1	2	0.5	0.5	2.8	2.6	9.6	19.6
61	*Dicranum scoparium*	10	20	+	–	+	–	0	0	0	0
34	*Pohlia nutans*	10	10	+	–	4	9	0	0	11.1	13.8
38	*Rhodobryum roseum*	10	70	+	–	+	–	0.2	0	0.2	0.1
51	*Plagiomnium cuspidatum*	0	50	0	0	+	–	0	0	1.0	1.7
39	*Brachytecium curtum*	20	90	+	–	5	6	1.7	–	25.1	32.2
52	*Placiothecium sp.*	0	30		0	+	–			2.4	3.6
35	*Rhytidiadelphus triquetrus*	20	0	+	–	0	0	0.2	0		
31	*Pleurozium schreberi*	100	90	13	17	5	9	35.7	44.6	6.2	6.5
32	*Hylocomium splendens*	100	90	62	51	7	12	47.4	36.0	11.1	18.5
55	*Peltigera canina*	0	20	0	0	+	–	0	0	0	0
57	*Cladonia fimbriata*	0	10	0	0	+	–	0	0	5.4	0
	Litter	–	–	–	–	–	–	810.9	222.3	355.1	129.1
	Means										
	Grasses	100	100	2	3	1	3	6.4	7.3	1.5	1.7
	Dwarf shrubs	100	100	2	3	2	2	10.5	16.0	6.2	7.9
	Field layer total	100	100	2	3	1	2	7.5	9.2	3.3	4.7
	Lichens	0	30	0	0	+	–	0	0	5.4	–
	Bryophytes	100	100	7	21	2	2	14.7	21.2	7.2	7.7
	Ground layer total	100	100	7	21	2	2	14.7	21.2	7.0	7.3

Coverage

The most common species in the virgin forest floor was *Hylocomium splendens*, its coverage being 62 % (Table 1). The next most common was *Pleurozium schreberi* (13 %). The most common species in the virgin field layer were *Vaccinium vitis-idea*, *Carex digitata* and *Deschampsia flexuosa*. Their coverage is about 10 %. *Deschampsia flexuosa* is the only species in the raked floor vegetation which has a coverage above 10 % (12 %). Most of the species in both areas had a coverage of ca. 1 %.

The greater heterogeneity of the raked forest floor vegetation compared to that of the virgin forest is also evident in the differences between the coefficient of variation for the per cent coverages of the plants.

The raked forest vegetation has a higher heterogeneity as regards the dry weights of the plant species than the virgin vegetation (Table 1).

Ecological preference of species

The position of different plant species in different habitats in the scale of variation in the environment was analysed by principal component analyse (Fig. 7), the solution of the two first factors being used. It was possible to separate the plant species according to two ecological axis: forest-meadow and favoured or depressed by raking.

Most mosses belong to those who thrive in shaded forest *(Hylocomium splendens, Rhodobryum roseum, Pleurozium schreberi, Rhytidiadelphus triquetrus, Dicranum polysetum)*. Some species are able to survive disturbance and may even favour it. Such mosses are *Barbilophozia barbata*, *Ptilidium ciliare*, *Plagiomnium cuspidatum* and *Plachiotecium* sp. The only bryophyta in our material which favours a meadow-like habitat is *Brachytecium curtum*.

Dwarf shrubs are perennial and are not very sensitive to raking. However, they seem to thrive better in undisturbed conditions.

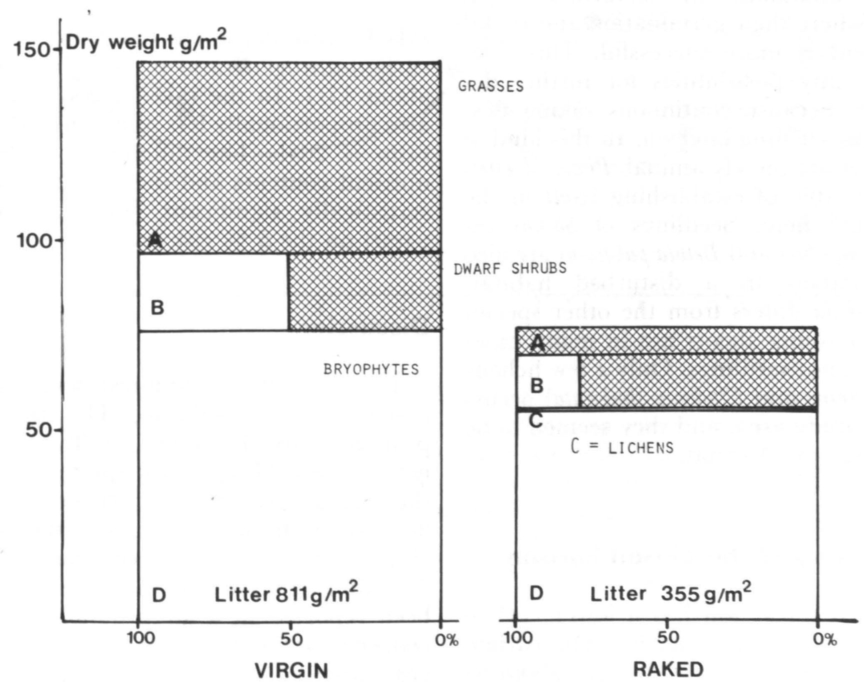

Fig. 5. Dry weights of the different plant life forms and litter in the virgin and the raked forest. A grasses, B dwarf shrubs, C lichens and D bryophytes. The proportion of the dotted area of grasses and dwarf shrubs indicatec the percentage of the production.

Vaccinium vitis-idea and *Ramischia secunda* thrive well in shaded and undisturbed conditions. *Vaccinium myrtillus* and *Rubus saxatilis,* on the contrary, are species which favour meadow-like conditions without disturbance.

Most of the grasses clearly favour a natural meadow-like habitat, but there are also species which occur more abundantly in raked conditions and those which thrive better in shaded moss-dominated forests. Species most clearly prefering meadow habitats include *Fragaria vesca, Solidago virgaurea, Ranunculus polyanthemus.* Shade tolerant species include *Carex digitata, Luzula pilosa, Anemone nemorosa.* Among those which tolerate disturbance are *Campanula persicifolia* and *Antennaria dioeca.* However, most grasses seem to suffer from the heaviest disturbance. Such abundant species as *Deschampsia cespitosa, Galium album* and *Lathyrus pratensis* seem to be favoured by moderate disturbance.

Tree seedlings

Tree seedlings of different species are clearly more abundant in disturbed, open habitats, where their germination and initial development is more successful. This does not imply any possibilities for further development, because continuous raking destroys young seedling later on. In this kind of habitat they are merely annual. *Pinus sylvestris* is most capable of establishing itself in the case studied here. Seedlings of *Sorbus aucuparia, Picea abies* and *Betula pubescens* are also more abundant in a disturbed habitat. *Populus tremula* differs from the other species because its young shoots are in many cases sprouts and not seedlings. Only a few lichens (*Peltigera canina* and *Cladonia fimbriata*) occurred in the study area, and they seemed to be favoured by open habitat.

Characteristics of the Ah-soil horizon

The raked forest soil has a lower carbon and nitrogen content (Fig. 6). The carbon content of the virgin forest soil was about 52 µg/mg and in the raked forest soil about one fifth lower. The nitrogen content of the virgin forest soil was about 3 µg/mg and in the

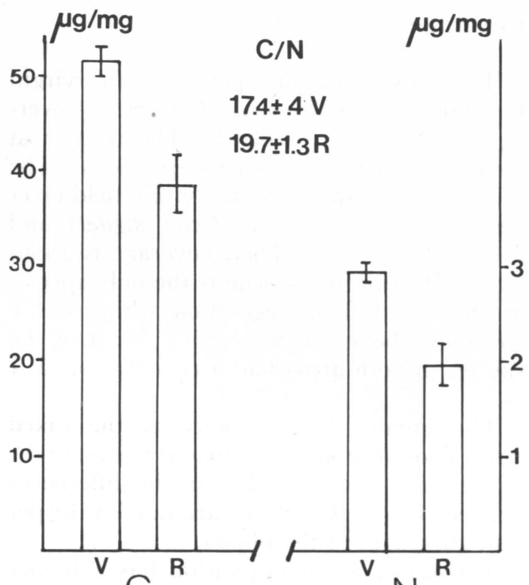

Fig. 6. The amount of carbon (C) and nitrogen (N) in the upper mineral soil layer of virgin (V) and raked (R) forest soil (N = 3) and C/N ratios. Asterisks indicate statistically significant differences in the amounts (t-test) and in the ratios χ^2-test), (p <0.05).

raked forest soil about one third lower. The carbon-nitrogen ratio in the virgin forest is about 17/1. In the raked forest soil there is also proportionally less nitrogen and the C/N ratio is 20/1. The differences both in the nutrient contents and their proportions were statistically significant (Fig. 6) (student's t-test) on the 5 % risk level.

Discussion

The structure of the forest floor vegetation is sensitive to disturbance. The species compositon is not, however, totally replaced by new species. Many forest species survive. In the raked area there is, however, a clear decrease in the above-ground biomass at least (Fig. 5). This implies suboptimal conditions. A similar deterioration in the production has been reported in a large number of studies concerning the stress exerted on the floor vegetation in coniferous forests (Kellomäki 1973, 1977, Kellomäki & Saastamoinen 1975 and Nylund et al. 1979) and also in heathlands (Bayfield 1973, 1979, Bayfield &

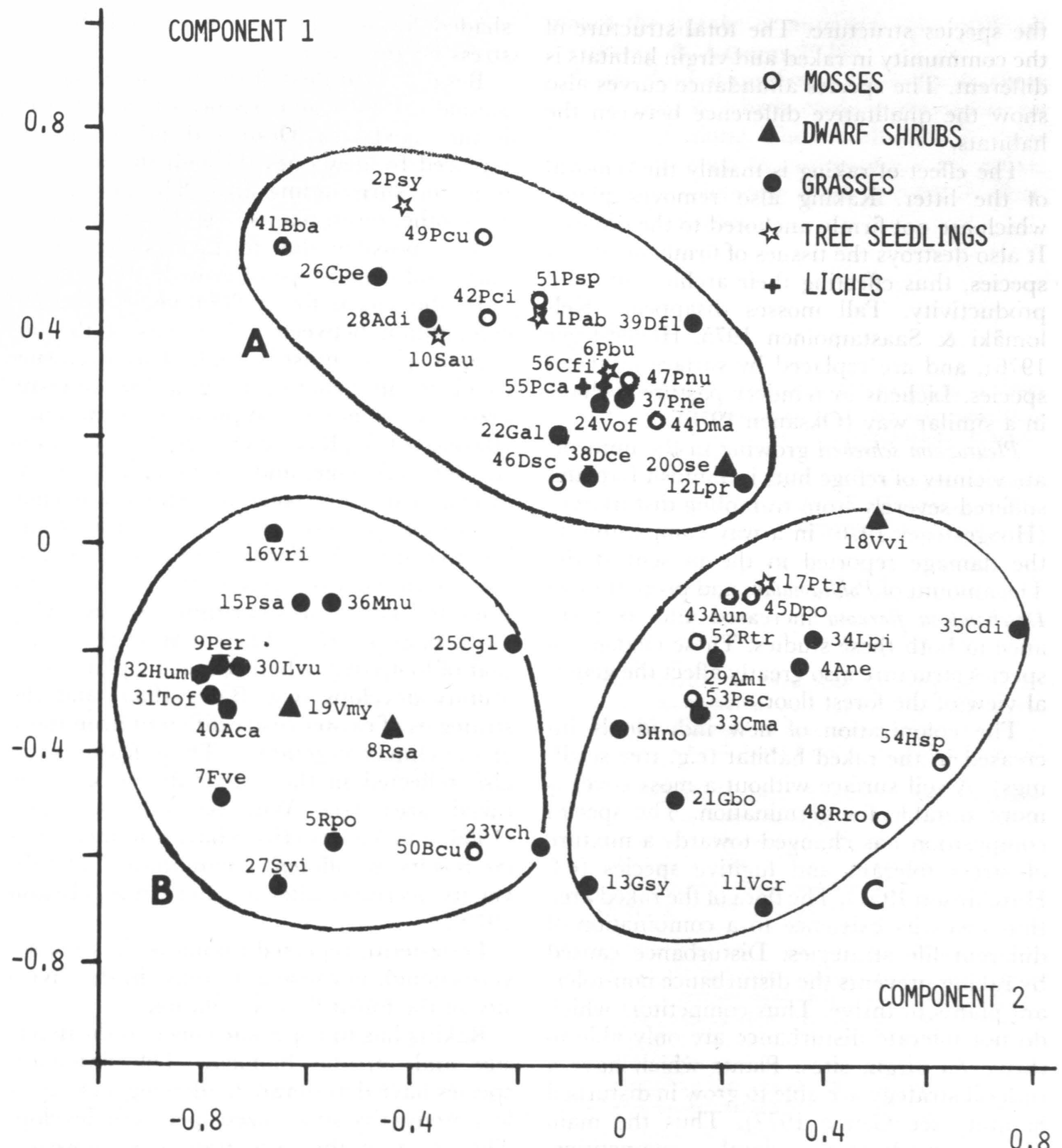

Fig. 7. The position of different plant species in a coordination of the two factor solution of principal component analyse. Factor 1 is considered to be a measure of the amount of disturbance in the habitat. Factor 2 is considered to be a measure of the transition between meadowish and moss dominated shaded habitats. The species codes are based on their latin names (see Table 1). The three major ecological groups are separated by eye: A species tolerating of favouring disturbance, B species favouring meadowish forest, C species favouring moss-dominated forest.

Brookes 1979 and Harrison 1981). An increase in production after disturbance has also been shown (Liddle 1975). In this case a low intensity of disturbance results in an increase in species richness. In this study the stress is, however, too heavy to permit any increase in the standing crop.

The decrease in the biomass is merely a result of deterioration of the individual plant species. It is also partly a result of a change in the species structure. The total structure of the community in raked and virgin habitats is different. The species abundance curves also show the qualitative difference between the habitats.

The effect of raking is mainly the removal of the litter. Raking also removes plants which are not firmly anchored to the ground. It also destroys the tissues of firmly anchored species, thus effecting their architecture and productivity. Tall mosses disappear (Kellomäki & Saastamoinen 1975, Hoogesteger 1976), and are replaced by surface attached species. Lichens in reindeer pastures behave in a similar way (Oksanen 1978).

Pleurozium schreberi growing in the immediate vicinity of refuge huts in Finnish Lapland suffered severely from trampling disturbance (Hoogesteger 1976) in a way comparable to the damage reported in the present study. The amount of *Pohlia nutans* and proportion of *Deschampsia flexuosa* increased after disturbance in both these studies. These changes in species structure also greatly affect the general view of the forest floor.

The colonization of new individuals increased in the raked habitat (e.g. tree seedlings). A soil surface without a moss cover is more suitable for germination. The species composition has changed towards a mixture of stress tolerant and fugitive species (c.f. Hutchinson 1951). The flora of the raked area thus owes its existence to a combination of different life strategies. Disturbance caused by raking prevents the disturbance non-tolerant plants to thrive. Thus competitors which do not tolerate disturbance are only able to thrive on virgin sites. Plants which have a ruderal strategy are able to grow in disturbed habitat (see Grime 1977). Thus the main strategy gradient is ruderal – competitive. Competition can be understood here as the tendency of neighbouring plants to use the same natural resources (e.g. Grime 1973). Ruderals are disturbance tolerant species which have a capacity for high rates of dry weight production and rapid completion of the life-cycle (e.g. Grime & Hunt 1975). In this study, two different situations (see Fig. 7) for competitive species (C strategy) can thus be discerned: shaded virgin forest and open virgin forest. The ruderal (R) strategy is favoured in the raked area. There may also be to some extent a stress (C) strategy in the shaded forest, where the lack of light is a stress for the plants.

Besides great deal of the tree seedlings are annual or their age is reduced to some years in the raked area. Destroyed individuals are replaced by new ones through the seed rain from the surrounding area. The presence of some other forest plants (e.g. dwarf shrubs) is mainly possible due to their subterranean parts and clonal type of growth.

In the virgin forest floor vegetation, the competition between individuals of the dominant species must be high. The succession trend is, in general, from a low-diversity phase to a more complicated community (Bazzaz 1975). Raking changes the system to successional stage, and the periodicity of the mechanical disturbance prevents the normal succession process. However, in this study the diversity is higher in the raked area. The species abundance curve is also further away from the curve of logarithmic series (May 1975, Bazzaz 1975). The situation resembles that of footpaths, where a specific plant community develops (e.g. Bates 1935) and the strategies of existence are different from those of the climax vegetation. These features are also reflected in the higher diversity of the raked area (see Whittaker 1975). Paine (1966) and Yodzis (1977) have obtained similar results in different communities. The diversity decreases after harsher stress (Huston 1979).

Long-term, repeated raking is thus not severe enough to cause a decrease in the diversity of the forest floor vegetation.

Raking has the opposite effect on the diversity and on the biomass. The dominant species have deteriorated, allowing a group of less productive small sized species to develop. The cover of the vegetation has, however, decreased after raking.

The community in the raked area is mostly composed of sparse mosses and a few vascular plants. In more fertile soils the low grass vegetation can be dense in case where there is a low degree of disturbance (e.g. yard lawns) if the disturbance increases gradually (Hoogesteger 1976).

Litter removal also imposes an indirect stress on the vegetation. The amount of nutrients decreases (McLeod et al. 1979, this study). This is due to the removal of organic matter and is exaggerated by the changes in the community structure of soil organisms (Harvey et al. 1980, Scowalter et al. 1981). The N/C ratio of the soil in the raked area is less favourable for nitrogen uptake than in the virgin control area (Black 1968). The soil also dries out more easily after litter removal and the uptake of water thus becomes more difficult (Ginter et al. 1979). Dryness also makes the uptake of nutrients more difficult (Witkamp & Ausmus 1976).

In the flora of coniferous forest floors, there are no species which could compensate for the effect of raking. The establisment of a new denser vegetation by cultivation of trampling and raking tolerating grass species fertilization and irrigation.

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