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Effect of forest management on alpha diversity of ground vegetation in boreal forests: a model approach

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The effect of various forest management types on the alpha diversity of ground vegetation was studied with an ecological simulation model. With this model, stand characteristics were simulated during different management programmes and were then used to calculate the diversity of the ground vegetation. Alpha diversity was expressed as Simpson's reciprocal, which was estimated using stand attributes. The diversity model was estimated using generalised linear models (GLMs). The significant variables in the diversity model were site type, stage of development (clearcut area or other), stand basal area and proportions of pine, aspen and willow as number of stems. In alternative management programmes, the type, interval and intensity of thinning were varied. In managed forests, the most intensive thinning produced the highest diversity of ground vegetation during a rotation. Differences in the diversity of ground vegetation between management programmes were, however, small.

Introduction

The dominant natural feature of the boreal vegetation zone is coniferous forests, which are therefore important for biodiversity. Forest management smooths out the variation in natural structures of forest stands by homogenising the age- and size distributions as well as the tree species composition (Esseen *et al*. 1992, Larsen 1995, Uuttera *et al*. 1997). A decrease in the structural diversity of trees also decreases the diversity of other species (Rescia *et al*. 1994, Larsen 1995, Uuttera *et al*. 1997) since the number of habitats decreases. However, Attiwill (1994a, 1994b), Rescia *et al*. (1994), Butterfield (1995) and Halpern and Spies (1995) stated that low-intensity forestry which results in forests with several tree species and variation in structural patterns can promote diversity. Nevertheless, no exact information is available concerning the impact of forestry on species diversity.

In previous studies, the environmental factors found to affect the species diversity of ground vegetation have been soil fertility (e.g. Kuusipalo

1985b, Økland and Bendiksen 1985, Tonteri 1994, Økland 1996, Pitkänen 1997), concentration of soil nutrients (Pausas 1994), soil moisture (Lahti and Väisänen 1987, Nieppola and Carleton 1991, Økland and Eilertsen 1993, Økland 1996, Graae and Heskjær 1997), and altitude (Økland and Bendiksen 1985). In addition, Kuusipalo (1985b), Tonteri *et al.* (1990) and Pitkänen (1997) found that crown cover, stand basal area and age affect species diversity. Other stand attributes that have an impact on diversity are tree species composition (Kuusipalo 1985b, Tonteri *et al.* 1990) and successional stage (Tonteri 1994, Pitkänen 1997). These factors that describe stand structure are of great interest when the effect of management on species diversity is evaluated.

Biodiversity can be expressed as alpha, beta and gamma diversities. Alpha diversity refers to species richness within an area (Whittaker 1972), e.g. a forest stand. This includes species richness and evenness of species abundances. Beta diversity is the rate of species turnover along an environmental gradient (Whittaker 1972, Wilson and Shmida 1984). Gamma diversity, in turn, refers to biodiversity at the landscape level and describes the number of species of different communities in an area and the level of differentiation of the communities (Whittaker 1972). Many ecological studies have concentrated mainly on measures of alpha and beta diversities and the impact of various environmental factors on these diversities. Alpha diversity can be described as species richness (Zobel *et al.* 1993, Tonteri 1994, Rey Benayas 1995) by alpha diversity indices (Zobel *et al.* 1993, Rescia *et al.* 1994, Tóthmérész 1995) or species presence (Nieppola 1992).

Experimental research concerning the effect of management on ground vegetation is difficult, expensive and time-consuming. An easier way to study the long-term effects of management on diversity of the ground vegetation is simulation. Simulation models have been used, e.g. to predict the habitat quality of flora (Botkin 1993) and fauna (Pausas *et al.* 1997). With a simulation model it is possible to study management alternatives and how they affect biodiversity. On the other hand, a simulation study shows gaps in knowledge and the need for empirical research.

The aim of this study was, using simulations, to examine the impact of forest management on the alpha diversity of ground vegetation. An interesting question was: Is it possible to maintain or increase the diversity of ground vegetation in commercial forests? In alternative management programmes, the intensity, interval and type of thinning were varied. One of these management programmes represents the current management practice in Finnish commercial forests.

Methods

Ecological simulation model

Alternative management programmes and their effects on stand characteristics were simulated with an ecological simulation model. This model is a nonspatial gap model based on the SIMA model (Kellomäki *et al.* 1992), which has been further developed in order to allow the study of biodiversity (Kolström 1998). In gap models, the death of a canopy tree creates a gap, which then becomes a site of regeneration and growth (Shugart 1984). The simulation model includes six tree species: Scots pine *(Pinus sylvestris* L.), Norway spruce (*Picea abies* Karst.), pendula birch (*Betula pendula* Roth), pubescent birch (*Betula pubescens* Ehrh.), European aspen (*Populus tremula* L.) and grey alder (*Alnus incana* Moench, Willd.). In this study, however, grey alder was omitted.

Growth of a tree is based on potential diameter growth, which is limited by multipliers describing the availability of temperature, soil moisture, nitrogen and light (Kolström 1998). The potential diameter growth of deciduous trees is high when the trees are young and decreases as they age. The diameter of conifers, on the other hand, grows more slowly when the trees are young and more rapidly when they are older (Kolström 1998).

The most important factor affecting the proportion of tree species in a stand is the growth factor for light. The value of the growth multiplier for light represents the shade tolerance of the tree species and the relative amount of light. The amount of available light is based on the amount of shading leaf area (Kolström 1998). Deciduous trees and Scots pine are shade intolerant and produce relatively little shade; while Norway spruce has a medium tolerance to shading, and shades more than deciduous trees or pine does (Ellenberg 1988).

The amount of nitrogen available in the soil depends on litter decomposition. The leaf litter of deciduous trees has more nitrogen and decomposes faster than does the leaf litter of conifers. On the other hand, the ability to use nitrogen for growth varies between tree species; thus the amount of nitrogen modifies the proportion of the various tree species in a stand. Soil moisture is based on the water-holding capacity of the soil type. In this study, simulations were made for gravelly till, which has a field capacity of 25% and a wilting point that is 5% of the dry weight of soil. Temperature is a growth factor which limits the geographical distribution of a tree species along the temperature gradient. The value of the temperature factor is based on the local climate, which in this study represents the climate of southern Finland (data from the meteorological station in Tampere, 61°25´N, 23°35´E). The climate data (temperature and precipitation) are entered into the simulation model as monthly means and their standard deviations (Kellomäki *et al.* 1992).

The simulation model includes the possibility to simulate silvicultural treatments. During the rotation there can be several treatments which form the management programme. In this study, twelve alternative management programmes were simulated; these included three types of thinning (the tallest (thinning from above) or the shortest trees (thinning from below) or trees of all heights were thinned), two thinning intensities (50% (high) or 30% (low) of the number of stems) and two thinning intervals (20 (short) or 40 (long) years). Each programme has an indicator (Table 1), in which the first letter indicates type of thinning (T = thinning from the tallest trees, S = thinning from the shortest trees, A = thinning from trees of all heights), the second letter indicates intensity of thinning (H = high, L = low) and the third letter indicates interval of thinning (S = short, L = long). In addition, one programme was simulated to mimic a Finnish thinning type (FTT in Table 1) in which small trees were cut first until the target basal area was reached and the thinning intensity was 33% of the basal area. This programme follows the instructions given to private forest owners in Finland (Luonnonläheinen metsänhoito 1994).

Each programme started from the situation after clearcutting. Since gravelly till is suitable for growing spruce, seedlings of spruce were planted in the beginning of the simulation and the other species regenerated naturally. The effects of thinning type, interval and intensity on the diversity of ground vegetation were studied with alternative programmes (Table 1). The thinning intensity determined the proportion of stems removed, and the thinning interval determined how many years there were between thinnings before simulation year 100. The total simulation time was 120 years.

In the model, the simulation area is 100 m^2, but results are given per hectare. The model includes many stochastic processes, such as the birth and death of trees; therefore to obtain stable results, the simulations were repeated 300 times. The results for the stand characteristics are averages of the iterations, and these averages were also used to calculate the diversity of the ground vegetation with a diversity model, which was included in the simulation model.

The alpha diversity model

The alpha diversity model of Pitkänen (1998) was used to describe the impact of stand characteris-

Table 1. Thinnings in alternative management programmes.

Indicator of programme	Type of thinning Thinning from	Intensity (%)	Interval (years)
TLS	the tallest trees[1)]	30	20
THS	the tallest trees	50	20
TLL	the tallest trees	30	40
THL	the tallest trees	50	40
SLS	the shortest trees[1)]	30	20
SHS	the shortest trees	50	20
SLL	the shortest trees	30	40
SHL	the shortest trees	50	40
ALS	trees of all heights	30	20
AHS	trees of all heights	50	20
ALL	trees of all heights	30	40
AHL	trees of all heights	50	40
FTT	basal area, from below	33	45, 60[2)]

[1)] The tallest trees are those whose height is 80%–100% of the tallest tree in the stand; the shortest trees are those whose height is less than 80% of the tallest tree in the stand.

[2)] These numbers indicate thinning years from the beginning of the simulation.

tics on diversity of vegetation. This model was estimated on the basis of data collected during the Eighth National Forest Inventory in Finland. The data consisted of 289 circle plots on mineral soil sites and included detailed information about the site and tree stand as well as the ground vegetation on the plots. All plots were in managed forests. The tree stand and site measurements included information on the topography, slope, site fertility, soil type, forest management procedures, number of crown layers, basal area, dominant tree species, mean diameter of trees, stand age and damage (e.g. by wind or insects). The trees on the plot were determined to species, diameter was measured at breast height, the crown layer to which the tree belonged was identified and the manner of regeneration was recorded (Metsäntutkimuslaitos 1985a). For sample trees, some additional variables (tree height, diameter at six metres, age, breadth of the crown and detailed information on the quality of the crown) were measured. The ground vegetation was measured on six sample squares (each 2 m^2) placed on the tree stand sample plots. Each species of the vegetation was identified, and species abundance was measured as percentage cover (Metsäntutkimuslaitos 1985b). A total of 295 species were detected.

The alpha diversity of the vegetation was described as Simpson's reciprocal (Krebs 1989) and represented the total diversity of the vegetation, including bottom, field and shrub layers but excluding the tree layer. Simpson's reciprocal is one of the first heterogeneity indices (Whittaker 1972, Krebs 1989), and with this data it was found to be an effective index for discriminating between stands (Pitkänen 1998). The diversity model was estimated using generalised linear models (GLMs), which have been found to be flexible enough for ecological purposes (Hastie and Tibshirani 1986, McCullagh and Nelder 1989). GLMs are estimated using estimation of maximum likelihood. Due to the possibility of combining different error and link functions for estimating the parameters, GLMs effectively describe any nonlinearity in the data. To estimate the diversity model, normal and gamma error functions, both of which are suitable for continuous variables, were used together with identity, reciprocal and logarithmic link functions. The best result was obtained with a combination of normal error and identity link functions (Pitkänen 1998); i.e. with this model the lowest deviance and the highest explained deviance were obtained. The response variable, Simpson's reciprocal, is non-linearly related to the explanatory variables; thus a logarithmic transformation was needed (Pitkänen 1998).

The explanatory variables were selected by a procedure of backward elimination. In this procedure the variables are removed from the model one at a time; and if the reduction in deviance caused by this is significant, the variable is put back into the model (McCullagh and Nelder 1989). The significant explanatory variables in the diversity model were site type (value of 1 if *Oxalis-Myrtillus* type, otherwise 0) and stage of development (1 if clearcut area, otherwise 0), the stand basal area and proportions of pine, aspen and willow of the number of stems (Table 2). The diversity model explained only 26% of the variance of the response, probably due to the fact that other environmental factors also have a great effect on diversity, and these factors were not measured in the data. In addition, processes like competition between and within species affect diversity; but here no information about such processes were included in the data. With this diversity model, however, it is possible to examine the direction of the change due to the treatments and to determine which treatments would produce the greatest impact.

Results

Thirteen management programmes were simulated; and using these, the alpha diversity of the ground vegetation was studied (Fig. 1). In each programme, the diversity of ground vegetation was the same in the beginning. During the two first years, the dummy-variable stage of development (Table 2) had a value of one, and Simpson's reciprocal (SR) had a value over eight. After those two years, the value of SR decreased and after year 20 started to vary among the programmes.

The diversity of ground vegetation was highest when the stand was thinned equally from trees of all heights (the first letter of programme indicator is A). Differences in the diversity index were small between programmes in which trees of all heights were thinned and programmes in which the shortest trees were thinned (the first letter of

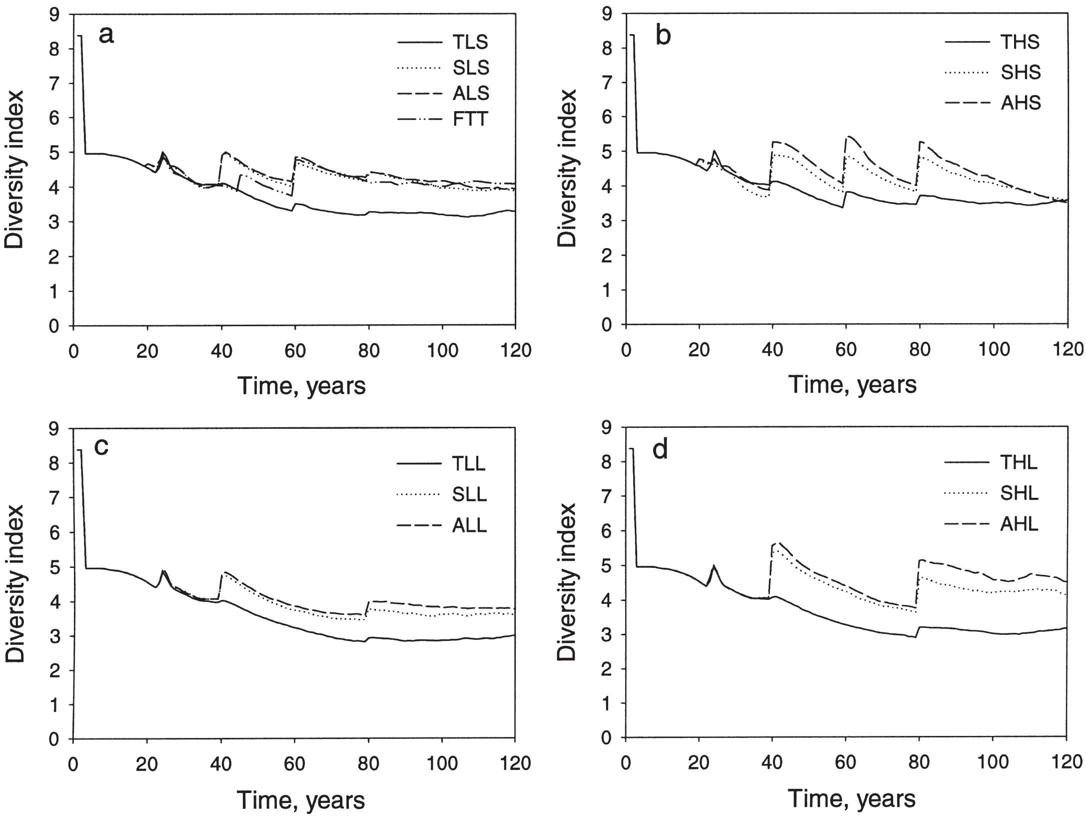


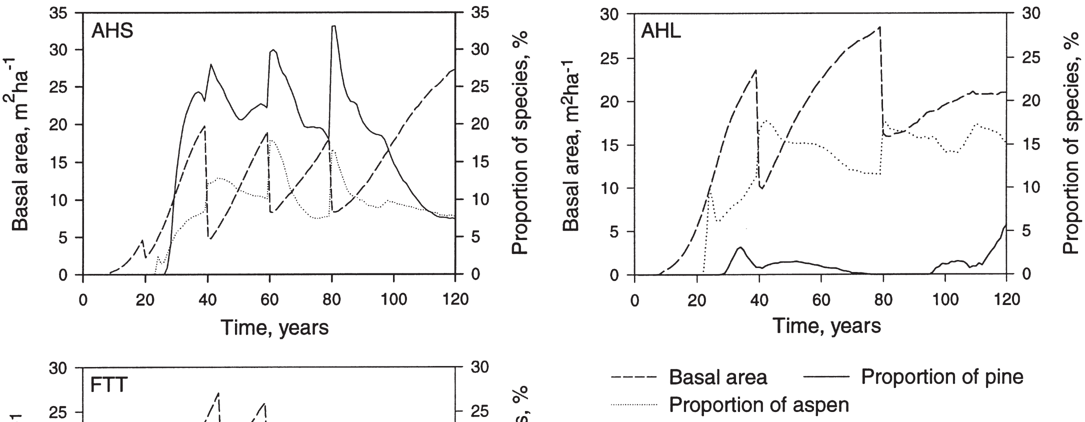
Fig. 1. Diversity index (Simpson's reciprocal) of ground vegetation in different management programmes. — a: Programmes in which thinnings were at short intervals, low intensity (30% of number of trees) and typical thinning from below (FTT). — b: Programmes in which thinnings were at short intervals and high intensity (50%). — c: Programmes in which thinnings were at long intervals and low intensity (30%). — d: Programmes in which thinnings were at long intervals and high intensity (50%). The first letter in programme indicator indicates type of thinning (T = thinning from the tallest trees, S = thinning from the shortest trees, A = thinning from trees of all heights).

programme indicator is S) (Fig. 1). The value of SR clearly differed between programmes in which the tallest trees were thinned and the other two types of thinning. The Finnish thinning from below (FTT) produced diversity similar to that produced in programmes in which trees of all heights

Table 2. Stand characteristics that affect the alpha diversity of ground vegetation. The response variable is log (Simpson's reciprocal).

Variable	Parameter estimate	Standard error	*t*-value
Constant	1.906	0.073	26.11
Site fertility[1)]	0.394	0.063	6.25
Stage of development[2)]	0.411	0.131	3.14
Basal area [m^2 ha^{-1}]	–0.012	0.003	4.00
Pine, proportion of number of stems	–0.191	0.070	2.73
Aspen, proportion of number of stems	1.251	0.483	2.59
Willow, proportion of number of stems	–0.835	0.402	2.08

[1)] Value is 1 if *Oxalis-Myrtillus* site, otherwise 0
[2)] Value is 1 if clearcut area, otherwise 0



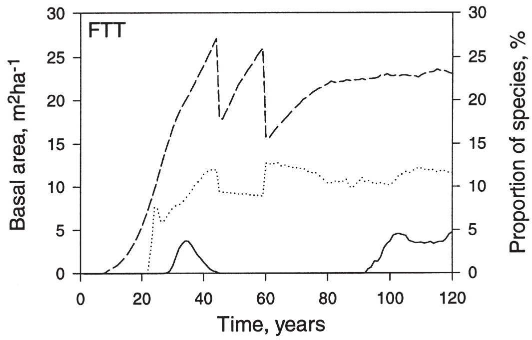


Fig. 2 (above and on the left). Factors of the diversity index model in three management programmes during rotation. AHS is a programme in which trees of all heights were thinned, the interval was short and the thinning intensity was high. AHL is a programme in which trees of all heights was thinned at long intervals and the thinning intensity was high. FTT is a programme with thinning from below.

or the shortest trees were thinned and where thinning interval and intensity were similar (Fig. 1a).

The effect of thinning interval on the value of SR was clear because diversity responded to thinning. A short thinning interval increased the value of SR more than a long interval did (*see* Fig. 1a vs. 1c or 1b vs. 1d). Especially when the thinning intensity was low, short intervals maintained higher values of SR than long intervals did (Fig. 1a and c). The effect of thinning intensity on the value of SR was also clear. High thinning intensity maintained higher diversities than low intensity did (*see* Fig. 1a vs. 1b and 1c vs. 1d).

Those programmes that produced the highest SR value by thinning type were compared with thinning removal according to volume (Table 3). The programme in which the tallest trees were thinned (THS) produced the smallest removal. Because of the small number of stems in height class 80%–100% of the tallest tree, proportional thinning intensity produces small removal of volume by thinning. In the programmes in which the shortest trees (SHS, SHL) and trees of all heights (AHS, AHL) were thinned, a short interval produced more removal than a long interval did. Typical thinning from below (FTT) produced slightly smaller removal than that in the programme in which the shortest trees were thinned at long intervals (SHL).

The effect of thinning interval on the diver-

Table 3. Removal by thinning in different management programmes.

Indicator of programme (*see* Table 1)	Removal of trees (m^3 ha^{-1})	Proportion of removal (%) of volume		
		Spruce	Pine	Aspen
THS	77	94	1	1
SHS	226	63	12	7
SHL	174	81	0	5
AHS	234	61	11	9
AHL	196	83	0	4
FTT	145	70	0	7

sity factors was studied by comparing the programmes in which trees of all heights were thinned and the thinning intensity was high (Fig. 2). With a short interval (AHS) the proportion of aspen was low, while the proportion of pine was high. The impact of both these factors decreased diversity, but changes in basal area due to thinning increased it. A long interval (AHL) led to a high proportion of aspen, but the proportion of pine was very low. In thinning, the basal area decreased and the proportion of aspen increased; and the impact of these two factors increased the diversity of ground vegetation. Similar effects were found with typical thinning from below (FTT).

Discussion

The effects of type, intensity and interval of thinning on the diversity of ground vegetation were studied with the help of an ecological simulation model and a diversity model. The main result was that the diversity of ground vegetation was highest in the stand which was thinned with a short interval and 50% of the trees of all heights were removed (AHS). In this management programme, the removal by thinning was also highest; the removal was mostly spruce but also included deciduous trees. The result was: thinning kept the stand basal area very low, and the stand reached 20 m^2 ha^{-1} basal area after the age of 100 years.

Differences in diversity between different management programmes were small (Fig. 1). Nieppola (1992) also found that in mature managed pine stands the changes in species composition were minor. Diversity of ground vegetation in programme FTT was very similar to that in programme AHS. In programme FTT, however, thinning removal was less than in programme AHS; but if regeneration cutting is carried out before year 120, the removal will be larger in programme FTT than in AHS. On the whole, timber production was also similar in programmes AHS and FTT.

The ecological simulation model was developed for studying stand structure and its changes due to management (Kolström 1998). This model simulates stand structure and the mean diameter growth in pure stands, which are comparable to measured stands. The simulation model gives realistic, and in some cases also accurate, results (Kolström 1998). Mixed stands were compared with the average proportion of tree species in Finland (Ilvessalo 1952). In the comparison it was found that on a mesic site, the proportion of aspen could be too high; but otherwise, the proportion of tree species was comparable to that on the measured stands (M. Kolström, unpubl.). In this study, the proportion of aspen varied from 0% to 18% due to thinning (Fig. 2), and on the mesic site the average proportion of aspen was 3% (Ilvessalo 1952).

When diversity indices are used to describe diversity, certain facts should be remembered. The indices do not take into account either changes in species composition or variations within species. Therefore, the indices are useful for comparing different areas but cannot be used to describe them. Further, the indices do not measure whether the species are rare or threatened or not. And finally, since most of the indices are dependent on species number, they can give an overestimate of the diversity if the number of species is unknown (Peet 1974). However, if these restrictions are kept in mind and the result of indices are interpreted carefully, reliable estimates of diversity can be obtained for comparison of different stands.

The alpha diversity model used here was developed for describing the stand attributes that affect diversity of vegetation (Pitkänen 1998). The significant variables in the index model were the same variables that discriminated between stands when they were classified with respect to diversity of vegetation (Pitkänen 1997, 1999). The stands were classified using different types of ordination and classification. Thus, it can be concluded that site fertility, stage of development, tree species composition and basal area are the stand attributes that affect the diversity of ground vegetation. Furthermore, when calculations were made with broader data collected in eastern Finland (Pitkänen 1998), the same stand attributes were found to affect diversity. Thus it can be concluded that those variables which have an impact on diversity of vegetation can be adequately described by the diversity model. The diversity model was able to explain only about 26% of the deviance. This is mainly due to the fact that different processes, such as competition and herbivory, have a great impact on diversity of vegetation; and these factors are not included in the model. With this model it is, however, possible to estimate the impact (positive/negative) of the significant stand variables on diversity and thus to compare different sites and treatments to each other. But the model does not reveal the whole pattern of diversity, which should be kept in mind — in addition to the fact that the model can be applied only to managed forests.

The three factors of the diversity index that changed due to thinning were basal area and the proportions of pine and aspen (Table 2). The diversity of ground vegetation increased mainly when the basal area of the stand decreased (Fig. 2). In most thinnings, the proportion of aspen increased at the same time. These two factors had a positive impact on diversity. On the other hand, the effect of the proportion of pine was not as important. The stand basal area indicates the amount of canopy coverage (Kuusipalo 1985a); and its effect on ground vegetation has also been shown, especially in spruce stands (Tonteri *et al.* 1990, Tonteri 1994, Pitkänen 1999). In a birch-spruce forest, where the crown cover is high, attenuation of radiation at the crown level is greater than in a pine forest, where the crown cover is small (Larcher 1983). In a forest, the factor that most often limits ground vegetation is light. In light shade-intolerant plants grow well; but in shade they have small leaves and shade-tolerant plant species gain ground (Packham *et al.* 1992). Thus the coverage of plant species varies depending on the amount of light.

The basic factors that affect the cover of ground vegetation or the number of species are, however, soil moisture and nutrient content (Kuusipalo 1985b). In the diversity model their effects on ground vegetation are indicated by site fertility and the proportion of pine and aspen (Table 2). The *Oxalis-Myrtillus* forest site type is rich in nutrients, and aspen grows well on these sites. Pine succeeds on xeric sites which are poor in nutrients; thus a large proportion of pine may indicate a site poor in nutrients.

Simpson's reciprocal varies from one to the number of species in the sample. The index value can be interpreted as the number of equally common species required to generate the observed heterogeneity of the sample (Krebs 1989). In this study, the value of the diversity index ranged from 2.8 to 8.4 (Fig. 1). In general, in mesic heath forests the number of species varies between 16 and 20, and this number is highest in young stands (Tonteri 1994, Pitkänen 1999). In this study, the diversity index decreased after clearcutting, and only thinnings increased it. The model of diversity index does not respond to the stage of a young stand in which there are both pioneer species and species characterising a dense stand.

On the whole, differences in diversity in the different management programmes were so small that no programme can be recommended as maintaining the diversity of ground vegetation better than the others. Thinnings from below, which in Finland are used in practical forest management, produce as high diversity as the other types of thinning studied in this paper. When the value of the diversity index is considered, it should be kept in mind that diversity indices do not take into account the changes in species composition (Peet 1974) due to, e.g. forest management. This has an important impact on diversity. Furthermore, the indices do not indicate the effect of changes on specific groups of species; e.g. the diversity measured with an index can be the same in two areas, but some valuable species of old-growth forests may have disappeared and been replaced with pioneer species. This may partly explain why the differences between indices of the different management programmes were so small. Nevertheless, Simpson's reciprocal is one of the most informative diversity indices (Peet 1974), and the method developed in this study can be used to compare different management programmes in terms of their effect on the alpha diversity of ground vegetation. The method was developed and used on the stand level, but in future it will be necessary to develop a similar method for the landscape level using gamma diversity.

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