Species Richness and Structure Variations of Scots Pine Forest Communities during the Period from 5 to 210 Years after Fire

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Postfire recovery of species diversity (including a number of species, entropy of species relative coverage (Shannon index of species diversity) was studied in lichen and green moss site types of Scots pine forests in the central part of the Kola Peninsula. The results obtained indicate the difference in the dynamics of characteristics of biodiversity of forest components during postfire recovery. The stabilization of separate components of forest community varies in time from 5–15 to 120–140 years after the fire. Characteristics of the dwarf shrub and herb stratum recovered and stabilized 5–15 years after fire, while the complete stabilization of characteristics of moss-lichen cover is observed in community with fire ages of 90–140 years. Species richness of tree stratum recovered 120–140 years after fire. Time of complete stabilization of species richness of the community was estimated 120–140 years after fire. The size of the area over which characteristics of the biodiversity were estimated effected the mean values and, in most cases, the character of variation of studied characteristics. Over an area of 1×1 m dynamics of characteristics of species diversity coincide in forests of the studied types. Regardless of forest type within the area of 100 m^2 species richness recovered 30 years after the fire (i.e 3–5 times earlier than the establishment of the complete stabilization of the forest structure). That means that floristic composition of the forest remained unchanged from 30 to 210 years after the fire.

Keywords postfire recovery, biodiversity, pine forest
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List of Symbols

N Number of species
H' Shannon index of species diversity
S_i The cover proportion of species i in comparison with the total coverage of the N species

1 Introduction

The process of recovery of vegetation cover after sudden external force is, by all appearances, the only mechanism available for the efficient retrieval of the stability of the biosphere.

Recovery time (i.e. the time period after whose expiration the community could be treated as stationary, climax one) is fundamental characteristic of vegetation. Studying the process of recovery makes it possible to determine both the character and rate at which the vegetation cover reacts to various disturbances.

In boreal forest ecosystem fires are very common; their recurrence is in the average of 40–100 years (Zakrisson 1977, Foster 1983, Engelmark 1987, Gromtsev 1993). The recovery time for the most of characteristics (excluding the tree age structure and the store of biomass) spans approximately 100–150 years (Siren 1958, Morneau and Payette 1989, Gorshkov 1995, Gorshkov et al. 1995). At the same time studies in recovery of vegetational cover, based on strict quantitative analysis are concentrated predominantly at the initial stages of succession (Shafi and Yarrangton 1973, Lindholm and Vasander 1987, Anderson and Romme 1991). In all except a few of works describing postfire plant chronosequence during the period of more than 200 years (Siren 1958, Zakrisson 1977, Black and Bliss 1978, Zjabchenko 1984, Sannikov and Sannikova 1985, Payette et al. 1985, Morneau and Payette 1989, Sannikov 1992, Engelmark et al. 1993) the questions of dynamics of characteristics of biodiversity are not given attention.

As noted by Tilman and Downing (1994), the majority of researches on problems of biodiversity is devoted to the theory and modeling. Only the small part (20–30 %) is submitted by experimental work and studies of natural objects.

Thus, dynamics of biodiversity of communities during their recovery after fires belongs to a problem, which so far remains opened. The necessity of empirical studies in this field is emphasized by many researchers (Payette et al. 1989, Drake 1990, Vanha-Majamaa and Lähde 1991, Parviainen et al. 1994, Parviainen 1995).

The purpose of the work – is to characterize dynamics of species density (i.e. number of species per the unit area) and the species structure of various forest components (tree stratum and the regrowth of tree species, dwarf-shrub and herb stratum and moss-lichen cover) in the process of 210-year postfire recovery.

As far as the characteristics of diversity essentially depend on the size of area over which they were estimated (Hopkins 1957, Kyrbi et al. 1986, Magurran 1992, Barkman 1993) in the work me analyzed characteristics, determined at the area of 1 m^2 and 100 m^2.

2 Material and Methods

2.1 Study Area

Investigations were carried out in the central and western parts of the Kola Peninsula (67°40'–68°00'N; 30°50'–34°50'E), predominantly at the territory of the Lapland Biospheric Reserve. The study area presents an elevated plain covered by deep sand deposits laid down by till and glacial meltwater during Pleistocene (Armand and Kudlayeva 1975). Mean elevation ranges between 400–500 m above sea level. Soils within the study area are of podzolic type with a low pH and contain low levels of inorganic nutrients and organic matter (Nikonov 1987). The average annual temperature is 0.5°C; the average July temperature, 14°C, and the average January temperature, –13°C (meteostation in the town of Monchegorsk). The annual precipitation is about 500 mm, with 30 % as snow. The average frost-free period is 104 days. (Scientific and applied reference book... 1988). The regional vegetation corresponds to the northern part of the Boreal Forest.

The level of air pollution determined by sulphur dioxide and heavy metals dust not exceeds that of the background (Barkan et al. 1990; Barkan 1993).

All studied forests are situated in the regions avoid from reindeer grazing (Bobok 1971, Semenov-Tjan-Shansky 1977), felling and other types of anthropogenic activity.

2.2 Objects

Studied pine forests correspond to three groups of types: I lichen (the share of lichens in the moss-lichen cover exceeds 70 %); II green moss–lichen (the respective share of lichens remains within 30–70 %); III green moss type (lichen share is below 30 % and that of moss exceeds 70 %).

Performed analysis of data collected has emerged a similar character of recovery process in forests from groups II and III; in this connection they were pooled to form one sample under the title "green moss type".

All studied pine forests are characterized by low productivity and poor species richness. The woodstand is either purely pine (*Pinus sylvestris* L.), or, has a sprinkling of spruce (*Picea abies* (L.) Karst., *Picea obovata* Ledeb.) or birch (*Betula subarctica* Orlova). Crown density of trees reaches 20–40 %. The average trunk diameter (of trees 120–150 years of age) is 15–30 cm at 1.3 m of height. Average tree height is 10–15 m. The undergrowth is usually absent, or remains within 1 %, if found. It may include *Populus tremula* L., *Salix caprea* L. and *Juniperus communis* L.

Regardless of the forest type, the main dominants of the dwarf shrub and herb stratum are species of two families: *Ericaceae* Juss. and *Empetraceae* S.F.Gray: *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* (L.), *V. myrtillus* (L.), *Arctostaphylos uva-ursi* (L.) Spreng. and *Calluna vulgaris* L.) Hull. The total projected coverage of the stratum amounts to 13 % in lichen type and 28 % in green moss type. Herbs present only 1 % and 3 % in the cover, respectively. The total number of species registered in all sites is 18 (9 species of dwarf shrubs and 9 species of herbs).

The total projected coverage by the moss-lichen cover in forests affected by fire more than 30 years ago reaches 70–90 %. The total number of lichen species amounts to 45, that of mosses – 34. In pine forests of lichen site type 40 years after the fire the ground cover is dominated by *Cladonia deformis* Hoffm., *C. cornuta* (L.). Hoffm., *C. crispata* (Ach.) Flotov and *C. gracilis* (L.) Willd. Within the time span from 60 to 100 years after the fire it is dominated by *C. mitis* (Sarnst.) Hale et W.Culb., *C. rangiferina* (L.) Nyl. and *C. uncialis* (L.) Wigg. *Cladina stellaris* (Opiz.) Brodo is the main dominant in the moss–lichen cover in forests when fire occurred over 120 years ago. The ground cover in pine forests of green moss site type up to 40 years after the fire is dominated by *Polytrichum* spp. and *Pohlia nutans* (Hedw.) Lindb.; the main dominants in forests with fire aged more than 60 years are *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum* spp.

2.3 Sampling Methods

Vegetation analysis was performed at 50 permanent sampling sites 0.1–1.0 ha of size. From twenty to one hundred 1 × 1 m plots, organized into blocks of four (so that 2 × 2 m squares were formed) were established in each sampling site along 2–4 parallel transect lines. The distance between blocks was constant for each given site and was equal to 7 or 10 meters. The projected coverage (in percentage) of each species was estimated at each plot using the frame divided into 100 squares of 10 × 10 cm. The smallest surface area registered for tree species approximated ~1 dm^2, that for species of the dwarf shrub and herb stratum, moss–lichen cover and the regrowth was 1 cm^2.

The postfire ages of the selected sites were 5, 30–40, 60, 90, 150 and 210 years. Fire dating was based on the tree ring chronology, using living trees with fire scars at the radial distance of 50–100 m from sampling site. The age of the last fire was taken to be equal to the difference between the current age of a tree and that at the moment of injuring. In each case being analyzed the age of the last fire, determined in at least 5 of the trees, was one and the same.

For quantitative characteristic of species di-

versity two indicators were used: the total number of species, and the Shannon index of species diversity in a community, that is the entropy of species relative coverage.

The Shannon index was defined as:

$$H' = -\sum S_i \ln S_i \quad (1)$$

where S_i corresponds to the cover proportion of species i in comparison with the total coverage of the N species (Odum 1971, Magurran 1988).

The number of species and the Shannon index were calculated over the area of 1 m^2 and 100 m^2. The area of 100 m^2 was made up by one hundred of 1 m^2 plots. The area characterized in that case averaged 0.1–0.2 ha.

2.4 Statistical Analysis

To process the data collecting principles of the single factor gradient analysis was used (Whittaker 1973 a, b). Correlation analysis (Zachs 1976) was performed to examine relationships between the values of characteristics involved and the fire age.

To avoid erroneous interpretation of the results due to uneven distribution of sites along the fire gradient (the number of sites for the particular fire age ranges from n = 2 to n = 12), two statistical criteria were simultaneously used: non-parametric technique of sample comparison after Tukey (quick Tukey test) and the one-way analysis of variance (ANOVA) (Fisher 1955, Tukey 1959, Afifi and Azen 1982). Differences between samples were assumed to be valid when they were significant according to both criteria.

Lines in figures link the average meanings for significantly different samples. When the differences between samples were not significant the lines illustrate the average meaning for polled sample.

2.5 Nomenclature

The nomenclature used follows Cherepanov (1995) for the vascular plants, Santesson (1993) for lichens and Ignatov and Afonina (1992) for mosses.

3 Results

3.1 Moss–Lichen Cover

3.1.1. Number of Species

In lichen pine forests maximal values of the average species number (N = 16) over the area 1 m^2 were found 10–40 years after fire (Fig. 1a). By 90 years after fire average species number reduced 2-fold and did not change any more. Significant differences were recorded between samples of averages for forests burned 7–40, 60 and 90–210 years ago (Table 1). Samples of averages for forests with fire ages of 90 and 210 years were not statistically different (Table 2).

In green moss type of pine forests (as well as in lichen site type) maximal values of average number of species (N = 15) over the area of 1 m^2 were recorded in forests burned 30 years ago (Fig. 1b). Further the values reduced 2–3-fold and stabilized 90 years after fire.

At the total area of 100 m^2 30 years after fire species number averaged 38 in pine forests of lichen site type and 31 in green moss site type (Fig. 2a, b) and stabilized afterwards. No significant changes in the number of species at the total area of 100 sq.m were detected between samples for forests of both types burned from 30–210 years ago (Table 2).

3.1.2. Shannon Index of Species Diversity

In lichen pine forests maximal average meanings of the Shannon index (H' = 2.0) for the samples of 1 m^2 were found in forests with fire age of 30 years. Later, values gradually decreased and stabilized 120–140 years after fire at H' = 0.5.

In pine forests of green moss site type over the area of 1 m^2 Shannon index has reached a maximum (H' = 2.0) about 30 years after fire, then dropped and stabilized 90 years after fire (Fig. 1d).

In pine forests of lichen site type over the area of 100 m^2 the character of variation of the Shannon index coincided with the post-fire dynamics of that index over the area of 1 m^2: maximal

Table 1. Summary table of non-parametric comparison of samples of averages of characteristics involved for forests with differing fire ages (Quick Tukey test).

n	Figure	Characte-ristics	Forest type	Periods compared i	ii	Test statistics T_1	T_2	$T_{corr.}$	T	Signi-ficance
1	1a	N	l	7–40	60	6	12	1	17	***
2	1a	N	l	60	90–210	12	11	–	23	***
3	1b	N	m	30–60	90–210	7	11	1	17	***
4	1c	H'	l	30–40	60–90	4	8	2	10	*
5	1c	H'	l	60–90	150–210	14	8	1	21	***
6	1d	H'	m	30–60	90–210	6	4	1	9	*
7	2c	H'	l	40	60–90	3	8	2	9	*
8	2c	H'	l	60–90	150–210	8	4	1	11	**
9	3a	N	l	60–90	150	14	2	6	10	*
10	3a	N	l	5–90	150	16	1	9	8	*
11	3a	N	l	5–90, 210	150	20	1	11	10	*
12	3c	H'	l	60–90	150	13	1	6	8	*
13	3c	H'	l	5–90	150	15.5	1	9	7.5	*
14	3c	H'	l	5–90, 210	150	19.5	1	11	9.5	*
15	5a	N	l	40–90	150–210	14	4	2	16	***
16	5b	N	m	40–90	150–210	4.5	4	1	6.5	**

Abbreviations: N – number of species; H' – the Shannon index of species diversity; l – pine forests of lichen site type; m – pine forests of green moss site type.
*, **, *** – asterisks denote significant differences between two samples compared at α = 0.05, α = 0.01, α = 0.001 respectively.
Statistics: T_1 – number of values in the second sample (involving the highest value for two samples compared) which are in excess of all values in the first one. T_2 – number of values in the first sample (involving the smallest value for two samples compared) being under all values in the second one. $T_{corr.}$ – correcting value at substantial [significant] ($n_2 > 3 + 4n_1 / 3$) differeces of samples compared (see Zachs 1976, Tukey 1958). T – Tukey test statistics.

index value was observed 30–40 years after fire, then it decreased and stabilized about 120 years after fire (Fig. 2c; Tables 1 and 2).

In pine forests of green moss site type Shannon index shifted to a value H' = 1.5 40 years after fire and stabilized afterwards (Fig. 2d; Table 2).

3.2 Dwarf Shrub and Herb Stratum

3.2.1. Species Number

Over the area of 1 m^2 species number stabilized 5–10 years after fire in both lichen and green moss site types of pine forests, averaging 3 and 4 respectively (Figs. 3a, b; Tables 1 and 2).

In all the studied forests the number of species at the total area of 100 m^2 reached a certain value as soon as 5–10 years after the fire (N = 7 in lichen pine forests and N = 9 in green moss ones) and did not change further on (Figs. 4a, b; Table 2).

3.2.2. Shannon Index of Species Diversity

The species structure of the dwarf shrub and herb stratum levelled down during the first 5–10 years after fire. The Shannon index was rather stable in both measured forest types as well in plots and in total areas (Figs. 3c, 3d, 4c and 4d).

The average meaning of the Shannon index per 1 m^2 plots approximated 0.6 in lichen and 0.8 in green moss site type of pine forests.

Over the total area of 100 m^2 index values stabilized at a level of about 1.3 in both forest types.

3.3 Tree Stratum and the Regrowth

3.3.1. Species Number

Maximal average number of tree species and regrowth (N~1) was observed in lichen pine forests burned 60–90 years ago (Fig. 5a) and 30–90 years ago – in pine forests of green moss site

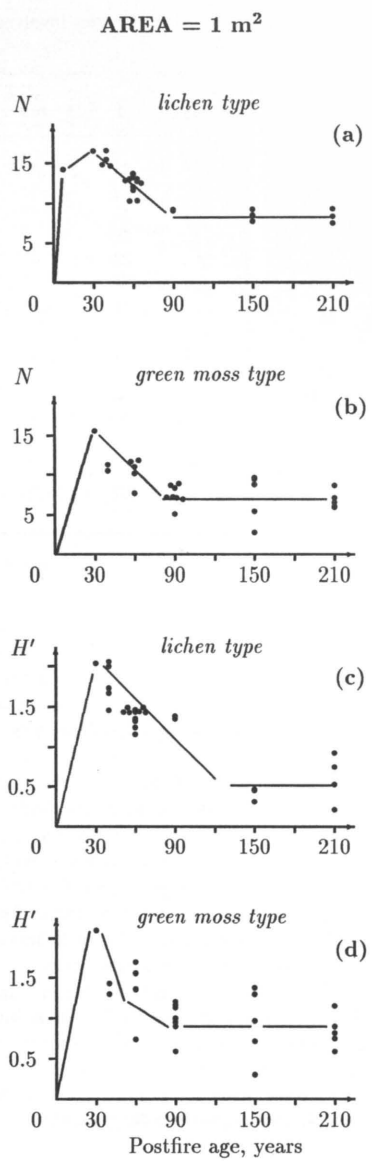

Fig. 1. Mean values of species number (N) and Shannon index of species diversity (H) of lichen cover in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (estimated over an area of 1 × 1 m).

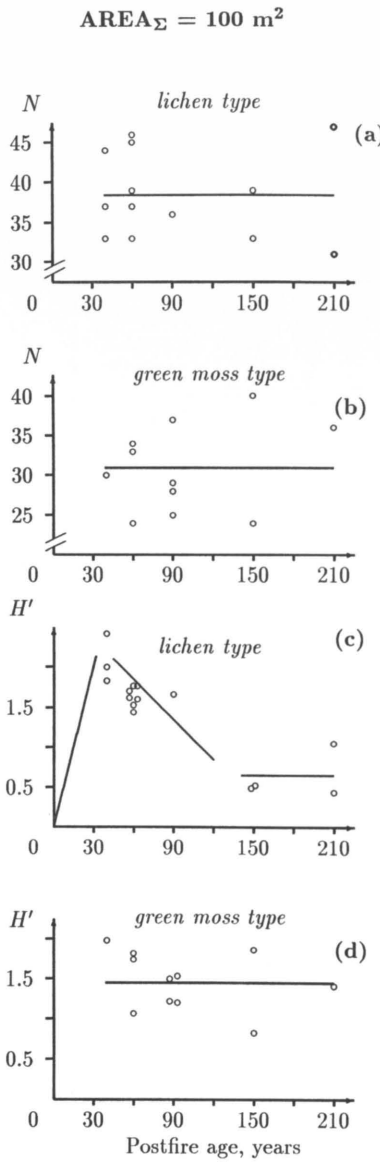

Fig. 2. Values of species number (N) and Shannon index of species diversity (H) of lichen cover in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (at the cumulative area of 100 m²).

Table 2. Summary tables of ANOVA.

n	Figure	Characte-ristics	Forest type	Postfire time span	Unit area	Statistics v_1	Statistics v_2	F-ratio	Signi-ficance
Lichen cover									
1	1a	*N*	l	90–210	1	2	7	0.58	
2	1b	*N*	m	90–210	1	2	17	1.00	
3	1c	*H'*	l	150–210	1	1	7	1.43	
4	1d	*H'*	m	90–210	1	2	17	0.96	
5	2a	*N*	l	40–210	100	4	11	0.66	
6	2b	*N*	m	40–210	100	4	4	0.24	
7	2c	*H'*	l	150–210	100	1	4	0.69	
8	2d	*H'*	m	40–210	100	4	4	2.90	
Dwarf-shrub and herb stratum									
9	3a	*N*	l	5–210	1	6	19	1.60	
10	3b	*N*	m	30–210	1	5	26	3.90	**
11	3b	*N*	m	30–210	1	1	30	0.39	
12	3ß	*H'*	l	5–210	1	6	19	1.86	
13	3d	*H'*	m	30–210	1	5	26	4.58	**
14	3d	*H'*	m	30–210	1	1	30	3.70	
15	4a	*N*	l	5–210	100	6	11	2.80	
16	4b	*N*	m	40–210	100	4	7	0.40	
17	4c	*H'*	l	5–210	100	6	11	0.80	
18	4d	*H'*	m	40–210	100	4	7	0.93	
Tree stratum and undergrowth									
19	5a	*N*	l	5–210	1	5	18	10.50	***
20	5a	*N*	l	150–210	1	1	4	0.61	
21	5b	*N*	m	40–210	1	4	15	3.14	*
22	5b	*N*	m	40–210	1	1	18	7.95	*
23	5b	*N*	m	150–210	1	1	5	0.33	
24	6a	*N*	l	5–210	100	5	11	0.95	
25	6b	*N*	m	40–210	100	4	3	0.03	
26	6c	*H'*	m	5–210	100	5	11	1.16	
27	6c	*H'*	m	5–210	100	1	15	0.65	
28	6d	*H'*	m	40–210	100	4	3	0.44	

Abbreviations: *N* – number of species; *H'* – the Shannon index of species diversity; l – pine forests of lichen site type; m – pine forests of green moss site type.
* – significant at $\alpha = 0.05$; ** – significant at $\alpha = 0.01$; *** – significant at $\alpha = 0.001$. Absence of asterisk denotes the lack of significant differences at $\alpha = 0.05$ (according to Fisher's test). Statistics: v_1 – degrees of freedom between groups; v_2 – degrees of freedom within group.

type (Fig. 5b). In both forest types the recovery of species number was detected 120–140 years after fire, approximating 0.6 in lichen type and 0.8 in green moss type.

At the total area of 100 ^{2} the average number of tree species and regrowth was 3 in lichen forest type and 4 in green moss forest type (Figs. 6a, b).

3.3.2. Shannon Index of Species Diversity

The average species density of trees and regrowth within the area of 1 m² is less than 1. It means that they were not present at each sampling plot. In those occasions the values of Shannon index for the area of 1 m² were not defined.

Recovery of the Shannon index over the total area of 100 m² coincided in time with the recovery of species density over that area (Figs. 6c, d) and was detected 5–15 years after fire. Mean

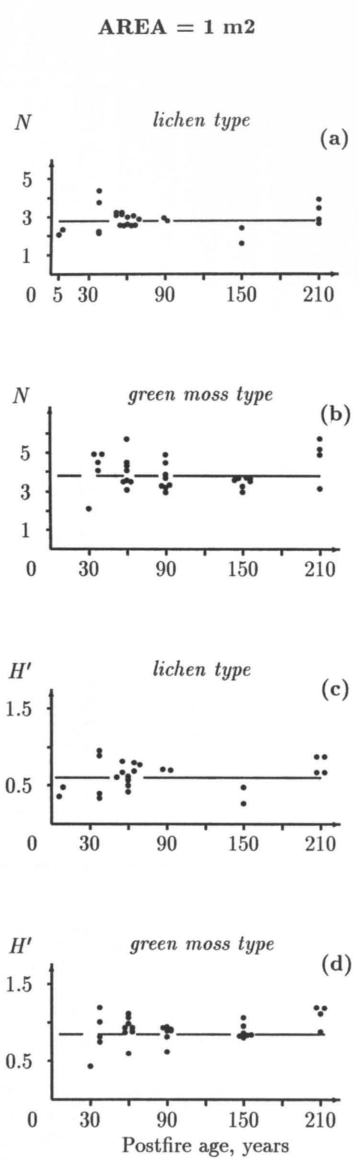

Fig. 3. Mean values of species number (N) and Shannon index of species diversity (H) of dwarf shrub and grass layer in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (estimated over an area of 1 × 1 m).

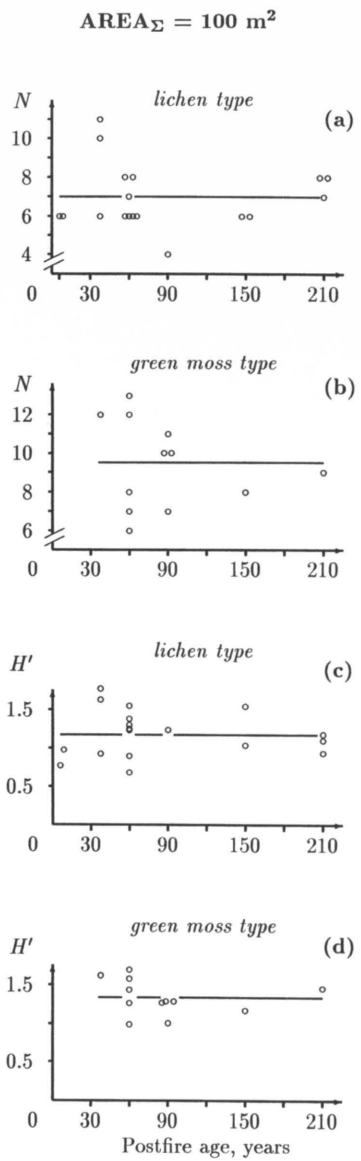

Fig. 4. Values of species number (N) and Shannon index of species diversity (H) of dwarf shrub and grass layer in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (at the cumulative area of 100 m^2).

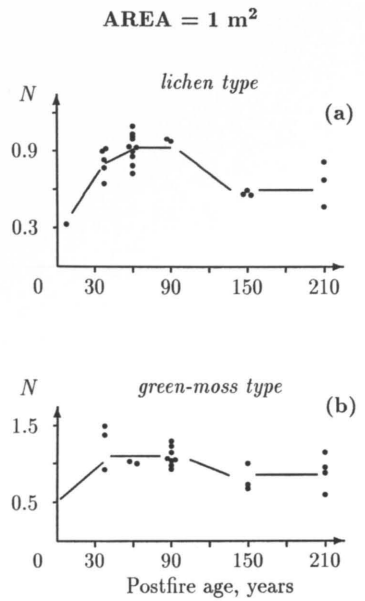

Fig. 5. Changes in mean values of number of tree species during postfire recovery in Scots pine forests of (a) – lichen site type and (b) – green moss site type in the Kola peninsula (estimated over an area of 1 × 1 m).

values of index averaged (H~0.2) in lichen and 0.5 in green moss forest type. No significant differences were evident between plots within the whole studied period.

4 Discussion

The results obtained indicate the difference in the dynamics of characteristics of biodiversity of separate forest components during postfire vegetative development (Table 3).

Characteristics of the dwarf shrub and herb stratum recovered and stabilized 5–15 years after fire, while the complete stabilization (restoration to its stationary non-perturbed state) of characteristics of the tree layer, regrowth and moss–lichen cover is observed in communities affected by fire

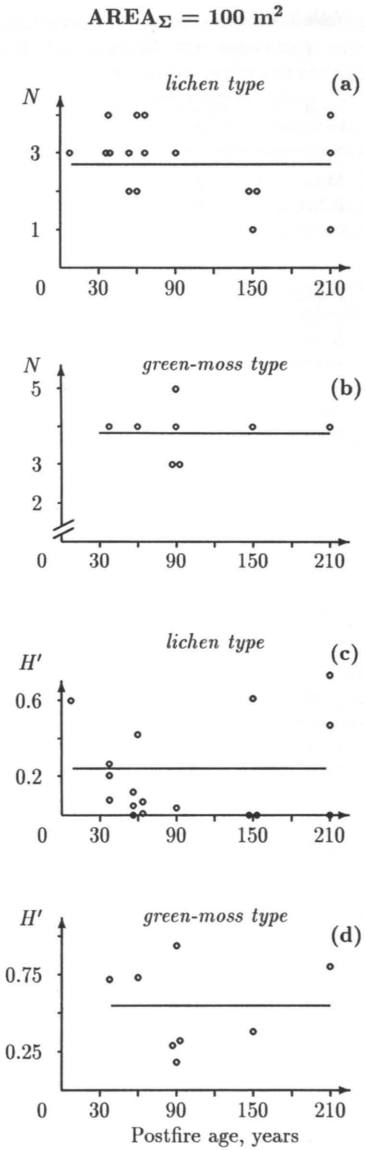

Fig. 6. Changes in values of species number (N) and Shannon index of species diversity (H) of tree species during the postfire recovery in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula (at the cumulative area of 100 m^2).

Table 3. Recovery time of characteristics of biodiversity in lichen and green moss types of Scots pine forests in the Kola peninsula. (Abbreviations – see Table 2)

Forest component	Characteristics Characte-ristics	Forest type	Recovery time On area: 1¥1m	A_{Σ} = 100 m²	Complete
Moss-	*N*	l	90	30	90
lichen	*N*	m	90	30	90
cover	*H'*	l	120–140	120–140	120–140
	H'	m	90	30	90
Dwarf	*N*	l	5–15	5–15	5–15
shrub	*N*	m	5–15	5–15	5–15
& herb	*H'*	l	5–15	5–15	5–15
stratum	*H'*	m	5–15	5–15	5–15
Tree	*N*	l	120–140	5–15	120–140
stratum &	*N*	m	120–140	5–15	120–140
regrowth	*H'*	l	–	5–15	5–15
	H'	m	–	5–15	5–15
Complete	*N*	l	120–140	30	120–140
	N	m	120–140	30	120–140
	H'	l	120–140	120–140	120–140
	H'	m	90	30	90

90–140 years ago. Therefore, time of complete stabilization of species richness of the community is approximated 120–140 years after fire.

Presented regularity of postfire restoration of characteristics of biodiversity is in general agreement with the process observed during post-fire succession elsewhere in Boreal Forest (Shafi and Yarranton 1973, Bazzaz 1975, Black and Bliss 1978, Southwood et al. 1979, Morneau and Payette 1989, Payette et al. 1995). Coincidence of the stabilization time of characteristics of biodiversity in different forest types and geographically isolated parts of boreal forest can not be accidental. It proofs that the recovery time of characteristics of biodiversity, approximating to 120–140 years, – is one of the fundamental characteristics of boreal forest communities.

The character of response (i.e type of relationship, mean value, location of maximum and the relaxation time) produced in species diversity significantly depends on the surface area from which such characteristics are retrieved.

The time of complete stabilization of characteristics of species diversity of communities is determined by the time of their restoration in the 1 m² sampling plots. On the total area of 100 m² stabilization of characteristics appears earlier or at the same time as in the 1 m² sampling plots.

Species density on the total area of 100 m² recovers quickly after fire, taking 30 years only, and then remains unchanged up to 210 years after fire (this is 3–5 times earlier than establishment of the complete stabilization of species density in the community as a whole). That means that floristic composition (the overall set of species of separate forest components) remains unchangeable from 30 to 210 years after fire.

Essential differences in the dynamics of species density and the entropy of relative coverage of species during post-fire regeneration, found at different area analyzed, indicates the existence of 2 levels of organization of the community: the interior, corresponded to the area of 1 m², the exterior, corresponded to the area of 100–400 m².

Structural replacement in vegetational cover is realized at the interior level. Period of complete stabilization of diversity characteristics at that level was found to be equal to 120–140 years after fire.

On the exterior level sustains the basic species set, necessary for the community functioning in recovery and stationary (climax) regimes. The period of recovery and stabilization of species richness at that level is not more than 30 years.

Acknowledgments

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