# BRYOPHYTES OF FRAGMENTED OLD-GROWTH SPRUCE FOREST STANDS OF THE NORTH KARELIAN BIOSPHERE RESERVE AND ADJACENT AREAS OF FINLAND

# МОХООБРАЗНЫЕ ФРАГМЕНТИРОВАННЫХ СТРОВОЗРАСТНЫХ ЕЛОВЫХ ЛЕСОВ БИОСФЕРНОГО ЗАПОВЕДНИКА СЕВЕРНАЯ КАРЕЛИЯ И ПРИЛЕГАЮЩИХ ТЕРРИТОРИЙ ФИНЛЯНДИИ

ANATOLY I. MAKSIMOV<sup>1</sup>, ALEXEY D. POTEMKIN<sup>2</sup>, TIMO J. HOKKANEN<sup>3</sup> & TATJANA A. MAKSIMOVA<sup>1</sup>

Анатолий И. Максимов $^1$ , Алексей Д. Потёмкин $^2$ , Тимо Ю. Хокканен $^3$  и Татьяна А. Максимова $^1$ 

Abstract

North Karelian Biosphere Reserve and adjacent areas of Finland were studied in 1996 – 2001 for bryophytes in 21 fragmented old-growth spruce forest stands. In total 194 bryophyte species (119 mosses and 75 liverworts) were recorded, including nine of Red List of Finland (Anastrophyllum hellerianum, Calypogeia suecica, Cephalozia macounii, Harpanthus scutatus, Herzogiella turfacea, Lophozia ascendens, Polytrichastrum pallidisetum, Riccardia multifida, R. palmata). The bryophyte flora is analysed with respect to species composition and distribution within the area, ecological groups and frequency of species. The groups of mosses and liverworts common for the North Karelian Biosphere Reserve and adjacent areas and conservation issues are considered. The main characteristics of the floras of studied spruce stands are connected with the amount of rotting wood, shaded rocky outcrops and presence of constant moisture and admixture of deciduous trees. Distinctive features of the flora are defined in comparison with the Central Norway spruce stands.

Резюме

В результате выполненных в 1996-2001 гг. исследований 21 участка фрагментированных старовозрастных лесов Биосферного заповедника Северная Карелия и прилегающих территорий Финляндии выявлено 194 видов мохообразных (119 мхов и 75 печеночников). Девять из выявленных видов (Anastrophyllum hellerianum, Calypogeia suecica, Cephalozia macounii, Harpanthus scutatus, Herzogiella turfacea, Lophozia ascendens, Polytrichastrum pallidisetum, Riccardia multifida, R. palmata) являются краснокнижными в Финляндии. В статье анализируются таксономический состав флоры, распространение мохообразных по территории исследования, экологические группы и встречаемость видов. Определены и обсуждены группы обычных и редких для территории исследования видов мхов и печеночников. Особенности флор мохообразных изученных ельников связаны главным образом с количеством гниющей древесины, затененных скальных выходов, постоянной влажностью и наличием примеси лиственных пород. Отличительные черты флоры выявлены при ее сравнении с флорой мохообразных ельников Центральной Норвегии.

#### INTRODUCTION

The bryophytes are an integral component of old-growth spruce forests. They form forest floor, cover logs, stumps, tree bases and trunks as well as rocky outcrops, abundantly grow near water courses and in wet depressions. Studies of bryophytes of spruce forests in Sweden and Norway (Gustafsson & Hallingbäck, 1988; Söderström, 1988; Hallingbäck, 1991; Frisvoll, 1997; Frisvoll & Prestö, 1997) show that bryophyte diversity is higher in old-growth than in young forests.

<sup>1 –</sup> Institute of Biology, Pushkinskaya str. 11, Petrozavodsk, 185610 Russia - Россия 185610 Петрозаводск, ул. Пушкинская 11, Институт биологии КарНЦ РАН (e-mail: maksimov@krc.karelia.ru)

V.L. Komarov Botanical Institute, 2 Prof. Popov Str., St. Petersburg, 197376 Russia – Россия 197376 Санкт-Петербург, ул. Проф. Попова, 2, Ботанический Институт им. В. Л. Комарова РАН (e-mail: Potemkin\_alexey@mail.ru)
 North Karelian Biosphere Reserve, P.O. Box 69, FIN 80101 Joensuu, Finland (e-mail: timo.hokkanen@ymparisto.fi)



Fig. 1. The study area.

Table 1. List of fragmented mature spruce forest stands of the North Karelian Biosphere Reserve and adjacent territories of Finland

Stand	Munici pality	Longitude	Latitude
Tapionaho	Ilomantsi	62°52'15''	31°27'60"
Lahnavaara	Ilomantsi	62°55'22''	31°32'47"
Koitajoki	Ilomantsi	62°55'23"	31°25'51"
Raiskionaho	Ilomantsi	62°59'24"	31°18'25"
Pampalo	Ilomantsi	62°59'55"	31°15'07"
Pampalo slope	Ilomantsi	62°59'55"	31°15'07"
Hoikka	Ilomantsi	63°01'29"	31°21'14"
Lakonjärvi	Ilomantsi	63°01'35"	31°17'51"
Pyötikönkosket	Ilomantsi	63°01'41"	31°26'33"
Syväjärvi	Ilomantsi	63°01'48"	31°18'16"
Pieni Kotavaara	Ilomantsi	63°01'48"	31°22'40"
Pahkavaara	Lieksa	63°09'48"	30°55'16"
Suolamminvaara	Lieksa	63°19'18"	30°46'49"
Ukonsärkkä	Lieksa	63°19'18"	30°46'49"
Haapahaasianvaara	Lieksa	63°20'03"	30°44'02"
Päävaara	Lieksa	63°33'51"	29°48'30"
Piilopirtinaho	Valtimo	63°46'31"	28°26'03"
Salmivaara	Valtimo	63°47'41"	28°50'16"
Verkkojärvi	Valtimo	63°47'51"	28°42'57"
Murtovaara	Valtimo	63°48'28"	28°54'11''
Paistinvaara	Nurmes	63°49'18"	29°14'51"

Area of old-growth spruce fortests is deminishing in Finland. However, until present there were no available for international scientific community special studies on bryophytes of oldgrowth spruce forests of Finland. North Karelian Biosphere Reserve in eastern Finland, adjacent to the Russian border, is a part of UNESCO's research, monitoring and development network (UNESCO 2002), and the information from these areas is especially important from the international point of view. These facts stimulated our research project, which was initiated by T.J. Hokkanen in 1996 by selecting the sites from North Karelian old-growth spruce forests. In 1996-1997 all the studied sites were sampled for mosses and liverworts by A. I. Maksimov. T. A. Maksimova was involved in the project in 1998 to study mosses together with A.I. Maksimov. A. D. Potemkin joined the project to study liverworts in 1999. He identified all previous gatherings of liverworts, made his own collections in selected sites (Pieni Kotavaara, Syvajärvi, Pampalo, Pampalo slope) in summer 2001, 2003 as well as suggested and developed basic approaches to analysis of the bryophyte flora of the studied area in the course of preparation of this paper.

The goals of this paper are (i) to make an overview of bryophyte species composition in fragmented old-growth spruce forests of the North Karelian Biosphere Reserve and adjacent areas of Finland, (ii) to provide some features of distribution and ecological behaviour of bryophytes in the area, and (iii) to define some peculiarities of bryophyte flora of the studied Finnish fragmented old-growth spruce forests.

# STUDY AREA, MATERIAL AND METHODS

The forested areas of Finnish North Karelia as well as the rest of Finland consist of extensive cuttings, young forests and drained bogs. Oldgrowth forests are ± rare. North Karelian Biosphere Reserve and adjacent areas of Finland belong to the middle taiga zone, a little to the north of boundary between middle and southern taiga zones (Ahti *et al.*, 1968) (Fig. 1). The climate of the area is moderately continental. The average annual precipitation in period since 1961 till 1990 was 648 mm and temperature +2.1°C. The warmest month of the year, July, has average temperature + 15.8°C, the coldest, January, --11.9°C (Helminen, 1997).

Collections of bryophytes in the studied area were made in 21 old-growth spruce stands situated in the North Karelian Biosphere Reserve and adjacent territories in Finland (Fig. 1, Table 1). The southernmost stand (Tapionaho) is situated in about 200 kilometres from the northernmost (Verkkojärvi). The area of studied stands varies from 8 to 61 hectares. The stands are 120-160 years old and should be attributed according to classification of A. K. Cajander (1926) to the spruce forests of Myrtillus type. Spruce (*Picea abies*) associates usually with pine (Pinus sylvestris) and birch (Betula pendula, B. pubescens), sporadically with willow (Salix caprea), aspen (Populus tremula) and rowan (Sorbus aucuparia).

The stands, considered most interesting from bryofloristic viewpoint (Pieni Kotavaara, Hoikka, Lakonjärvi, Syväjärvi, Ukonsärkkä), were investigated repeatedly. Some stands (Pahkavaara, Tapionaho, Pampalo slope) were investigated only partly because of unfavourable weather and/or short time for collecting. Moreover, stands Piilopirtinaho, Murtovaara, Koitajoki, Tapionaho, Pyötikönkosket were insufficiently studied with respect to hepatics. Taking into account uneven investigation of separate stands we pay attention to investigation of their common characteristics mainly and avoid their detailed analysis and comparison.

In every stand all recognized bryophyte habitats (Table 4) were repeatedly studied with respect to bryophyte species composition. Frequency, abundance and ecological preferences of the bryophytes were determined in the field wherever possible. The identification of every species was verified in the laboratory. Totally about 2000 bryophyte specimens were collected. Frequency of the species in separate stands was estimated using a five-grade scale: 1 – found 1-2 times in studied stand; 2 – found 3-6 times; 3 -7-15 times; 4-16-22 times; and 5- over 22 times (Table 3). For evaluation of species frequency in the studied area their frequency grades for separate stands were summarized. To define how regularly every species occurs in different stands the percentage of stands in which species was found was estimated. Ecological preferences of every species were defined as percentage of their frequency in recognized habitats (Table 4). To clarify which taxonomic groups play more

Table 2. Largest families and genera in the studied area and number of their species in the studied sites. Pa-Pahkavaara, Uk - Ukonsärkkä, Pä - Päävaaara, Pv - Paistinvaara, Pi - Piilopirtinaho, Mu - Murtovaara, Ve - Verkkojärvi, Ho - Hoikka, Sy - Syväjärvi, Pk - Pieni Kotavaara, Py - Pyötikönkosket, La - Lakonjärvi, Ta - Tapionaho, Ko - Koitajoki, Pm -Pampalo, Ps - Pampalo slope, Ha - Haapahaasianvaara, Sa - Salmivaara, Ra - Raiskionaho, Lv - Lahnavaara, Su - Suolamminvaara.

Families and genera

Stands and number of species

Pa	Uk Pä	Pv	Pi	Mu Ve	Но	Sy	Pk	Ру	La	Ta	Ko	Pm Ps	Ha Sa	Ra	Lv	Su	
----	-------	----	----	-------	----	----	----	----	----	----	----	-------	-------	----	----	----	--

	1 α	ОК	. 1 4	1 V	11	1.10	IVC	110	Бу	1 K	1 y	La	ıα	100	1 111	113	114	Sa	ita	LV	<u> </u>
						I	IЕР	ATI	CAl	Ε											
Lophoziaceae (19) Jungermanniaceae (9)	4	7	6	7	3	1	7	5	7 1	9 8	3	6	4	3	14 7	7	11	10	7 2	5	7
Cephaloziaceae (8) Scapaniaceae (6)		2	1				2 2	2	2	6 3	1	1	1		5 4		3	3	4	1	2
Calypogeiaceae (5) Geocalycaceae (5)	1	1	2	1	1	1	3	1 2	3 1	5 1	1	1 1	1	1	4	1	1	2	1 2	2	2
Lophozia (7)	1 2	3 1	3 1	3	2	4	3	2 2	3	4	2	3 2	1	2	6 4	3 2	6 3	5 3	4 2	2 2	3 3
Barbilophozia (6) Cephalozia (6) Scapania (6) Jungermannia (5)	2	2	1	3	1	1	2 2	2	2	3 5	1	1	1	1	4 4 4 3	2	3	3	4	1	2
Calypogeia (5) Riccardia (4)	1	1	2	1	1	1	3	1	3	5	1	1	1	1	4 3	1	1	2	1	2	2
Anastrophyllum (3) Nardia (3)	1	2	2	1				1	1	2		1	2		2 2	2	2	2	1	1	1
Cephaloziella (3)								1	1	2		1			2				1		
							M	USO	CI												
Dicranaceae (19)	6	11	9	9	5	8	7	8	11	7	9	7	6	8	13	5	7	7	8	5	5
Sphagnaceae (14)	7	9	6	7	5	6	7	8	7	10	6	5	7	4	9	3	5	9	10	9	4
Brachytheciaceae (10)	1	7 7	9	2 3	3 2	4	4 2	5 2	5 5	6	3	7 2	6	5	9	4	6	6 2	6	5 3	6 3
Polytrichaceae (9) Amblystegiaceae (8)	4 1	3	1	3 1	1	3	3	2	ა 3	4	3 4	3	3	1 5	7	ა 1	2	2	4	3 4	3
Hypnaceae (8)	1	3 1	2	2	1	3	2	1	2	2	1	1	2	4	4	3	3	2	2	2	1
Mniaceae (7)	1	2	1	2	2	2	1	2	2	_	1	1	1	1	7	J	3	2	2	1	1
Bryaceae (6)	2	1	1	1	2	2	1	2	2	2	1	1	1	1	4	1	3	2	1	1	1
Hylocomiaceae (5)	2	3	3	2	4	3	2	3	2	3	3	3	3	3	5	2	3	3	3	3	3
Sphagnum (14)	7	9	6	7	5	6	7	8	7	10	6	5	7	4	9	3	5	9	10	9	4
Dicranum (9)	5	7	6	6	4	6	5	7	7	6	5	6	5	7	7	5	5	6	6	5	5
Brachythecium (6)	1	5	6	1	3	4	4	5	5	5	3	6	6	5	5	4	6	6	6	5	5
Dicranella (4)	1	3	1		1	1		1	1	1	2		1		2	-	1	-	2		
Plagiothecium (4)	1	2	2	2	1	1	2	3	1	1	1	1	1	1	3	1	3	2	2	1	1
Pohlia (3)	2	1	1	1	2	2	1	1	2	2	1	1	1	1	2	1	2	1	1	1	1
Polytrichum(3)	2	2	1	1	1	1	2	1	2	3	2	1	1	1	2	2	2	2	2	1	2
Plagiomnium (3)		1	1					1	1			1	1	1	3		1	1	1	1	1
N of bryophyte species		66	57	46	35	45	53	56	68	91	40	49	51	41	140		63	62	66	47	44
N of moss species	29	50	44	36	29	39	36	40	44	47	33	35	43	35	85	27	41	41	47	36	29
N of liverwort species	8		13	10	6	6	17	16	24	44	7	14	8	6	55	14	22	21	19	11	15
Moss/liverwort species	s 3.6	J.1	3.4	3.6	4.8	6.5	2.1	2.5	1.8	1.1	4./	2.5	5.4	5.8	1.5	1.9	1.9	2.0	2.5	3.3	1.9

significant role in old-growth spruce forests the taxonomic sorting and analysis of species list were carried out (Table 2). These approaches provide the basis to analyse species composition with respect to their frequency in separate stands, in all stands together and in regularity of species occurrence in the studied area.

Our data are roughly comparable with Frisvoll's (1997) study on bryophytes of spruce forest stands of Central Norway. The author studied bryophytes from 110 spruce stands of different age with particular emphasis on oldgrowth forest. Unfortunately the list of bryophytes of Central Norway spruce stands was not segregated with respect to age of spruce stands. This made impossible to reveal the species composition of the old-growth spruce stands *per se*, which is important for a proper comparison. The species lists of Finnish and Central Norway spruce stands were analysed with respect to their taxonomic composition, differential species composition, ecological and geographical distribution of differential species, and species frequency.

Circumscription of families and genera of mosses is accepted after Ignatov & Afonina (1992), of hepatics – after Grolle & Long (2000), except families Scapaniaceae and Diplophyllaceae treated after Potemkin (1999) and genus *Chiloscyphus* after Engel & Schuster (1984). Nomenclature of mosses follows to Söderström (1996, 1998), liverworts to Grolle and Long (2000), mainly. Representative collections are allocated in Herbarium of Botanical Museum, University of Helsinki (H), Herbarium of the Institute of Biology, Petrozavodsk, Russia, and liverworts partly in Herbarium of V.L. Komarov Botanical Institute, St. Petersburg, Russia (LE).

#### RESULTS AND DISCUSSION

#### TAXONOMIC COMPOSITION

Totally 119 moss and 75 liverwort species were recorded in fragmented old-growth spruce forests of the North Karelian Biosphere Reserve and adjacent territories of Finland. The liverwort species of this flora belong to 29 genera and 19 families. The families Lophoziaceae, Jungermanniaceae, Cephaloziaceae, Scapaniaceae, Geocalycaceae and Calypogeiaceae include 19, 9, 8, 6, 5 and 5 species respectively. Other liverwort families are represented by 1-4 species. The largest genera in the flora are Lophozia (7 species), Barbilophozia, Cephalozia, Scapania (6 species), Jungermannia, Calypogeia (5 species). The other genera are represented by 1-3 species. Comparison of the species numbers of families and genera of different stands shows common and distinctive features of their species composition. The species of the families Lophoziaceae (especially of the genera Lophozia and Barbilophozia), Calypogeiaceae (Calypogeia), Ptilidiaceae (Ptilidium), and in less extent of Trichocoleaceae (Blepharostoma) appear to be most constant components of different fragmented old-growth spruce forest stands of the middle taiga zone of NE Finland.

The moss species of the studied old-growth spruce forests belong to 64 genera and 26 families. The families Dicranaceae, Sphagnaceae, Brachytheciaceae, Polytrichaceae, Hypnaceae, Amblystegiaceae, Mniaceae, Bryaceae are richest in the flora (Table 2). They include 19, 14, 10, 9, 8, 8, 7, and 6 species respectively. The family Hylocomiaceae includes 5 species. Species of families Dicranaceae, Sphagnaceae and Hylocomiaceae are common dominants in the forest floor. The genera *Sphagnum*, *Dicranum*, *Brachythecium*, *Plagiothecium*, *Dicranella* comprise largest number of species in the flora, i.e., 14, 9, 6 and 4 respectively. The other genera are represented by 1-3 species.

# NUMBER OF SPECIES IN STANDS

Number of bryophyte species of the studied stands varies considerably from 35 (Piilopirtinaho) to usually 40-68(-91) and up to 140 species recorded for *Pampalo* (Table 2). Such a considerable difference in species number results from the habitat diversity of stands and a difference in degree of their investigation. The stands, which have only small admixture of aspen (e.g., Pieni Kotavaara) have fewer moss species due to absence of substrate for species associated with aspen. The influence of aspen abundance is, however, indistinct in liverwort species number because there are no hepatics obligatory associated with this tree in the studied territory. The other important factor of bryophyte diversity is an abundance of wetland habitats. It leads to dominance of several species of Sphagnum, prevents distribution of the other species of mosses and creates habitats for some hepatics associated with Sphagnum. In drier stands the number of the liverwort species is considerably lower than that of the moss species. Occurrence of rocky outcrops affects much on bryophyte species diversity due to inclusion in the flora of numerous species associated with rocky habitats. Estimations of species numbers in separate stands show that in cases of their rather detailed investigation they have usually from 44 (Suolamminvaara) – 47 (Lahnavaara) to 68 bryophyte species (Syväjärvi) (Table 2). Moss/liverwort species ratio in them varies from 1.8 to 3.3 and is predetermined primarily by their moisture and the proportion of microhabitats of mosses and liverworts rather than by degree of investigation of both groups.

Species							Star	nds	and	l sn	ecie	es f	reai	1en (	ev s	rad	es				
Species	Pa	U	k Pä	Pv	Pi													a Sa	Ra	ı Lı	Su
Anastrophyllum hellerianum		1							$\frac{2}{2}$	2	)	1	1			1	1	2		1	1
Anastrophyllum minutum	2	2	2	2					2	1		1	1		2	1	1	1	1	1	1
Anastrophyllum saxicola	_	_	1	_						1			1		1	1	1	1	1		
Anthelia juratzkana			•												1						
Barbilophozia attenuata	3	3	3	3			2	1	3	2	2	1	2	2		1	2	2	3	2	2
Barbilophozia barbata	0	0	0	1			_	-	1	_	_	•	_	_	2	1	2	2	0	_	1
Barbilophozia floerkei				_					_	1					_	_	_	_			-
Barbilophozia lycopodioides	2			2	2	2	2	1	2	2		1			1		2	2	1	2	2
Barbilophozia ňatcheri							1								1						
Barbilophozia kunzeana							2		1												
Blasia pusilla										1					2						
Blepharostoma trichophyllum	2	2	2	2	2	2	2	2	1	2				2	2 3 3 2	2	2	2	1	1	1
Calypogeia integristi pula	2	3	3	1	3	2	1	2	2	3	1	1	3	2	3	2	1	3	3	2	1
Calypogeia muelleriana							1		1	2					2						1
Calypogeia neesiana									2	2					2			1		1	
Calypogeia sphagnicola			1				2			1											
Calypogeia suecica										1					1		1				
Cephalozia bicuspidata		1						1	1	2				1	3		1	1	1		
Cephalozia connivens															2				1		
Cephalozia leucantha			0				0			1					1		1	1		0	1
Cephalozia lunulifolia s.l.		1	2				2	1	1	1		1	1		2		1	1	4	2	1
Cephalozia macounii							4			4									1		
Cephalozia pleniceps							1			1									1		
Cephaloziella elachista								4	1	. 1						2					
Cephaloziella elegans								1	1c			4			2	2					
Cephaloziella rubella								1		1		1			2				1		
Chiloscyphus profundus		1						1	1	1					1		1	1	1		
Chiloscyphus profundus Cladopodiella fluitans		1						1	1	1					1		1	1	1		
Cladopodiella francisci										1					1						
Di plophyllum obtusifolium									1	2					1						
Di plophyllum taxifolium						1	2		1	_					1						
Geocalyx graveolens						•	_								1						
Gymnocolea inflata		1													•						
Harpanthus flotowianus												1									
Harpanthus scutatus															1						
Jungermannia caespiticia										2					2						
Jungermannia confertissima										1											
Jungermannia gracillima										1					1						
Jungermannia hyalina										1					2						
Jungermannia sphaerocarpa										1											
Leiocolea heterocolpos															1						
Lepidozia reptans	2	2	2					2	1	2					2	1	1	2	1	2	1
Lophozia ascendens										_					3		1				
Lophozia bicrenata										2					1		1				
Lophozia incisa							0								1			1			
Lophozia longidens	2		1		2	,	2	0	1			1		1		1	1	1	1		1
Lophozia longiflora s.l.		1	1	1		1	1	2	2	1	1	1	1	4	2	1	1	1	1	1	1
Lophozia obtusa		2	2	4	2		4	1	1	2	4	4		4	1	4	1	1	1	2	0
Lophozia ventricosa s.l.		2	2	1	2		1		2	3	1	1		1	2	1	2	3	1	2	2
Marsupella emarginata										4	1										
Marsupella spručei			1							1					4						
Metzgeria furcata			1							2					1				1		
Mylia anomala Nardia insecta									1	2 3					3				1		
Nardia insecta Nardia japonica									1	1					1				1		
Nardia japonica Nardia scalaris										1					1						
Pellia cf. neesiana										1					1						
i ciiia ci. necsiana															1						

	Pa	Uŀ	ς Pä	Pv	Pi	M	uVe	Но	Sv	Pk	Pv	La	Ta	Ko	Pr	n Ps	На	ı Sa	Ra	Lv	Su
Pellia epi phylla											J				1						
Plagiochila asplenioides s.str. Plagiochila porelloides		2						2	1 2			1 1			2	1	1	1			1
Ptilidium ciliare	2	4	2	2	2	2	2	1 3	1 3	1	1	1	2		2	1	1 3	1	4	2	,
Ptilidium pulcherrimum Radula complanata	3	4	3	3	3	3 1	3	Э	3 1	3		1 2	3		2	Э	5	4	4	3	4
Riccardia cf. chamaedrifolia								4		1					1	4					
Riccardia cf. multifida Riccardia latifrons								1							1	1					
Riccardia palmata										4					1						
Scapania curta Scapania irrigua							1			1					2						
Scapania lingulata															3						
Scapania cf. mucronata Scapania paludicola										1					1						
Scapania undulata							1				1				0						
Tritomaria quinquedentata						ΜŪ	JSC	CI							2						
Amblystegium serpens						2		1		1	1	1	1	1	1		1	1		1	1
Amblystegium subtile Amphidium lapponicum										1					1					1	
Andreaea rupestris			1	1			1						,		1				,		
Atrichum undulatum Aulacomnium palustre	1	1		1	2		2	2	1	1	2	1	1 2		2		1	2	2	1 2	
Bartramia ithyphylla			2	2											1						
Bartramia pomiformis Brachythecium erythrorrhizon			2	2			1	1	1			1	1	1	1		1	1	1		1
Brachythecium oedi podium		1	1 2		4	1		1	2	2	1	1	1	1	1	1	2	1	1	1	1
Brachythecium reflexum Brachythecium salebrosum		1 2	3		1 2	1 2	3	1	1 2	2	2	1 2	2 2 2	1	3	1 2	1	1	3	2	1
Brachythecium starkei	1	2	2	1	3	1	3 1	2	1	2	1	1	2	2	3	2	2	2	2	2	2
Brachythecium velutinum Bryum flaccidum		1	1				1			1		1	1		1		1	1	1	1	
Bryum pseudotriquetrum Callicladium haldanianum														1	1						
Calliergon cordifolium														1	1						
Campylium chrysophyllum Campylium sommerfeltii		1	1			1	1		1	1	1	1	2	1	1			1	1	1	1
Ceratodon purpureus		1	1			1	1	1	1	1	1		2	1	1	2		1	1	1	1
Cirri phyllum piliferum Cnestrum schistii												1			1						1
Cynodontium strumiferum			2	1			1		1						1						
Cynodontium tenellum Dicranella cerviculata	2	2	1	2	2	2		2	1 2	3			2		1		1		1		
Dicranella crispa		1									1										
Dicranella grevilleana Dicranella heteromalla		1									1				1				1		
Dicranum bergeri		4		4				4	4	4		1			1			4	4	4	4
Dicranum drummondii Dicranum flagellare		1		1				1	1	1		1		1				1	1	1	1
Dicranum flexicaule	,	2	1 3	,	,	2	1	1	1	1 4	1	1	1	1 2	1	1	2	2 3	2 3	3	3 4
Dicranum fuscescens Dicranum majus	4 5	3	3	4 5	4 5	5 5 2	4 3	1 3	3 3	3	1	2	3	1	3	2 3	2	3	3	3	4
Dicranum montanum Dicranum polysetum	1 5	1	1	5 2 5 3	5	2	5	5	1	5	1 5	5	3	1	1	4	1	3	3	3	
Dicranum scoparium	5 3	5 3	5 3	3	5 3	5 3	5 3	5 3	3 3	5 3	5 3	5 3	3	3 2	3	4 5	3 3	3 2	3 5	3	3
Ditrichum heteromallum Ditrichum pusillum										1									1		
Eurhynchium pulchellum			1							1					1						
Fissidens adianthoides Grimmia muehlenbeckii															1		1				
Hedwigia ciliata															1						
Herzogiella turfacea Heterocladium dimorphum	1								1						1	1					
Homalia trichomanoides					4				•						1						
Hylocomiastrum umbratum Hylocomium splendens	5	5	4	4	1 4	3	3	4	4	4	4	4	3	3	1 3	3	4	4	4	4	4
Hypnum cupressiforme						2															

	Pa	Ul	к Pä	Pv	Pi	M	uVe	Н	Sy	Pk	Ру	La	Ta	Ko	Pr	n Ps	На	s Sa	Ra	ı Lv	Su
Hypnum pallescens									1		·			1	1	1	1				
Isopterygiopsis pulchella Isothecium alopecuroides		1	2						1					1	2		1				
Isothecium myosuroides		2	3	2							4				1						
Kiaeria blyttii Mnium stellare											1				1						
Neckera oligocarpa			1												1						
Oligotrichum hercynicum Oncophorus wahlenbergii														1	1						
Orthotrichum obtusifolium				1	1	1	1		1			1	1	1	1						
Orthotrichum speciosum		1	1 2	2		2	1		1		2	2	2	3	1	1	1	1			
Paraleucobryum longifolium Plagiomnium cuspidatum		1	2	2		1	1		1		2	1	1	2	2		2	1	1	1	2
Plagiomnium elli pticum								1							2						
Plagiomnium medium Plagiothecium curvifolium		1						1							1		1				
Plagiothecium denticulatum	_		1	1		_	1	1		_		_	_		1		1	1	1		_
Plagiothecium laetum Plagiothecium piliferum	3	4	3	3	3	3	2	3	1	3	3	3	3	3	3	3	3	3	3	2	3
Pleurozium schreberi	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	5
Pogonatum dentatum	1	1		4	2	1			2	1	1		1		1	1			1		1
Pogonatum urnigerum Pohlia andalusica	2	2		1	2	2			2	2			2		2						
Pohlia cruda	2				2 2	2			1						1		1		_		
Pohlia nutans Polytrichastrum longisetum	2	3	3	2	2	2	2	1	2	3 1	3	1	1 2	2	2	1	2	3	3	3	3
Polytrichastrum pallidisetum		1				1			1				1							1	
Polytrichum commune	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	1 3	3	3	4	3	3
Polytrichum juni perinum Polytrichum strictum	1	1					1		1	3 1	5				1	5	2	1	1		1
Pseudobryum cinclidioides					2				3						3						
Pterigynandrum filiforme Ptilium crista-castrensis	4	4	3	3	4	4	3	1		3	2	4	3	3	1 4		3	2	3	2	3
Pylaisia polyantha	•	•	1	1	•	1	1	•	2	1	-	-	3 2	1	1	1	3	1	1	1	Ü
Racomitrium fasciculare Racomitrium microcarpon			2	1 2				1			1				2	1					
Rhizomnium pseudopunctatun	ı	1	4	_	2	1	1	2			1				1	1	1		1		
Rhizomnium punctatum						1		4							2		1	1			
Rhodobryum roseum Rhytidiadelphus subpinnatus								1							1		1	1			
Rhytidiadelphus triquetrus		3	3		3	2		3		2	3	1	2	2	3		2	2	2	1	1
Saelania glaucescens Sanionia uncinata	3	2	3	3	3	3	3	3	3	3	3	3	3	3	1	3	2	3	3	1	2
Schistidium papillosum			0	0	0		0	0	0	0					1	Ü	_	Ü	0	1	_
Schistostega pennata	1 2	1 3	1	1	2	2	2	2	1	1 3	1	1 2	2 3	2	2	1	1	1	1 2	2	1
Sphagnum angustifolium Sphagnum capillifolium	$\frac{2}{2}$	2	2	2	$\frac{2}{3}$	$\frac{2}{2}$	$\frac{2}{3}$	2	1	3	1	2	3	2	1	1	1	1	$\frac{2}{2}$	$\frac{2}{2}$	1
Sphagnum centrale		2				1		3	2	1	1	2			1			1	4	1	
Sphagnum compactum Sphagnum fallax		1	1					1					2					1	1		
Sphagnum fuscum	0	0		0	0	0	1	0	0	0	0	0		0	0		0	0	0	0	0
Sphagnum girgensohnii Sphagnum magellanicum	3	3	2	3	3	3	2 3	3	3 1	3 1	3	3	3	3	3 1	1	2	3	3	3 1	2
Sphagnum quinquefarium	1	1	1	1		1	2		1	2	$\frac{2}{2}$		1		1		1	1	1	1	1
Sphagnum ri parium Sphagnum russowii	2	3	2	3	3	2	3	3	3	1 3	3	3	2	2	3 1	1	1	2	1	1	
Sphagnum squarrosum	4	5	4	1		2	J	2	5	5	J	2	_	2	1	1	1	_	J	1	
Sphagnum warnstorfii	1	1		4	2			1 2		2					3			1	4	4	
Sphagnum wulfianum Splachnum luteum	1			1				2		2			1		1			1	1	1	
Splachnum rubrum													1								
Straminergon stramineum Taxi phyllum wissgrillii			2												1				1		
Tetraphis pellucida	1	2	2	3	3		1	3	2	1			3	3	2	2	2	3	2	2	2
Tetraplodon angustatus			1							1											
Tetraplodon mnioides Timmia austriaca										1					1						
Tortella totruosa							1								1				า		
Warnstorfia fluitans							1								1				2		

Two of the studied stands are much richer in species number than the others. They are *Pieni* Kotavaara (91 species) and Pampalo (140 species). Moss/liverwort species ratio in them is 1.1 and 1.5 respectively. This, however, results from more detailed studies of liverworts than mosses on bare and disturbed soil in these stands and from only small admixture of aspen in *Pieni* Kotavaara. Extreme richness of these stands in bryophyte species results from abundance of moist habitats and microhabitat diversity. So, the high rocks, which are constantly shaded by spruce forest in *Pampalo*, provide such a diversity of bryophyte habitats that number of species in this locality is 1.5-3 times higher than in the other stands.

Thus, among 21 studied old-growth spruce forest stands, the highest number of species have Haapahaasianvaara (63 species), Raiskionaho (66), Salmivaara (62), Syväjärvi (68), Ukonsärkkä (66), and particularly Pieni Kotavaara (91) and *Pampalo* (140). The species diversity of the studied stands is predetermined by degree of their microhabitat diversity, which correlates closely first of all with their moisture, presence of aspen, constantly shaded rocks and of rotten wood. It is noteworthy that number of species in the studied stands is not correlated with their area. Haapahaasianvaara, being the stand with the largest area - 61 ha, has 63 species, whereas the stands Pieni Kotavaara and *Pampalo*, having 91 and 140 species, have the area around 15 ha.

# FREQUENT SPECIES, SUBSTRATE AND RARITY

Comparison of the species lists of separate stands (Table 3) provides the basis to establish the "core species", which normally occur in the studied fragmented old-growth spruce forest stands. The most common liverwort species are Ptilidium pulcherrimum, Calypogeia integristipula, Barbilophozia attenuata, Blepharostoma trichophyllum, Lophozia ventricosa s.l., L. longiflora, L. longidens, Barbilophozia lycopodioides, Cephalozia lunulifolia, Lepidozia reptans. They were collected in most studied stands and have higher total frequency in comparison with the other species of the flora. Constant occurrence of these species in old-growth spruce forests appears to be connected with their wide distribution in taiga and predetermined by

correlation of their distribution with occurrence of habitats, which are characteristic of old-growth spruce forests (rotten wood, humid shady niches). 11 moss species occur in all 21 stands, whereas 5 species in 19-20 stands. Among them Pleurozium schreberi, Hylocomium splendens, Dicranum scoparium, D. majus, D. polysetum, Sphagnum angustifolium, S. girgensohnii, S. russowii, Polytrichum commune have a dominant role in the forest floor formation. The other species are insignificant in the forest floor formation and occur in the other habitats.

Analysis of ecological distribution (Table 4) shows that most liverwort species occur primarily on rotten wood (19 species) or on bare soil (17 species). Fewer species were found mainly in forest floor (14 species) or on boulders and rocky outcrops (7 species). Five species occur mostly at tree bases and among Sphagnum. Ecological distribution of mosses is different. 32 species were collected mainly on ground layer, 31 species on boulders and rocky outcrops, 14 on bared soil, 12 at aspen base and only five species were found mostly on rotten wood. Fewer moss species were collected on the other substrates (Table 4). A comparison of the revealed habitat distribution shows that the number of predominantly epixylic liverworts (19 species) is much higher than mosses (5); the number of saxicolous mosses (31 species) is considerably higher than liverworts (7); and the number of species growing at bases and bark of deciduous trees is significantly higher in mosses (17 species) than in liverworts (2). This appears to be resulted from different ecological preferences and strategy of liverworts and mosses, namely from stronger ability of liverworts than mosses to inhabit wet old logs characteristic of old-growth spruce forests and from weak ability of liverworts to grow on drier rocks, boulders. bases and bark of deciduous trees.

Nine species, which were included in Red Data Book of Finland (Rassi et al., 2001), are recorded in the study area. Most of them occur on rotten wood and bare soil. They are Calypogeia suecica, Harpanthus scutatus, Herzogiella turfacea (all vulnerable – VU), Cephalozia macounii (endangered – EN), Anastrophyllum hellerianum, Lophozia ascendens, Riccardia

Table 4. Distribution and frequency of bryophytes in habitats of mature spruce forests of the North Karelian Biosphere Reserve and adjacent territories of Finland. Abbreviations of habitats: FF – forest floor, BS – bared soil, AB – aspen base, BB – birch base, SB – spruce base, PB – pine base, RB – rowan base, WB – willow base, AS – aspen bark, BR – boulders and rocky outcrops, RW – rotten wood, SP – among *Sphagnum*, ED – elk droppings

Species	FF	BS	AB			uency RB V					ox.%) SP EI	)
			HEP	ATIC	AF.							
Barbilophozia floerkei	100											
Barbilopozia kunzeana	100											
Chiloscyphus polyanthos	100											
Harpanthus flotowianus	100											
Gymnocolea inflata	100											
Lophozia obtusa	100 100											
Pellia sp. (2 species) Plagiochila asplenioides s.str.	100											
Riccardia cf. chamaedrifolia	100											
Plagiochila porelloides	90								10			
Barbilophozia barbata	90		10									
Barbilophozia lycopodioides	80	10					10		_			
Barbilophozia attenuata	70				5				5	20		
Ptilidium ciliare	50								50	<b>50</b>		
Mylia anomala Tritomaria avinaved entata	50 50								50	50		
Tritomaria quinquedentata Scapania undulata	50 50								50 50			
Calypogeia muelleriana	40	30							50		30	
Lophozia longiflora	40	00			20					40	00	
Harpanthus scutatus		100										
Jungermannia species		100x5										
Lophozia bicrenata		100										
Nardia species		100x3										
Scapania curta		100										
Scapania irrigua		100 100										
Blasia pusilla Di plophyllum obtusifolium		100										
Cephaloziella rubella		80		20								
Di plophyllum taxifolium	30	70		20								
Calypogeia integristi pula		70					5			25		
Cephalozia bicuspidata	20	50								30		
Calypogeia neesiana		50								50	<b>=</b> 0	
Cephalozia pleniceps		50	20					70			50	
Radula complanata			30					70	100			
Anastrophyllum saxicola Metzgeria furcata									100			
Lophozia heterocolpos									100			
Scapania lingulata									100			
Scapania mucronata									100			
Anastrophyllum minutum									80	10	10	
Cephaloziella elegans	20								80			
Lophozia incisa var. incisa									50			
Carlypogeia suecica										100 100		
Cephalozia connivens Cephalozia macounii										100		
Geocalyx graveolens										100		
Lophozia ascendens										100		
Lophozia incisa var. inermis										100		
Riccardia latifrons										100		
Riccardia palmata									_	100		
Anastrophyllum hellerianum									5	95		
Lophozia longiflora var. guttulata			5	5	5				5 5			
Lophozia longidens Cephalozia leucantha	20		J	J	J				3	80		
Chiloscyphus profundus	20									80		
Riccardia cf. multifida	$\frac{1}{20}$									80		
Blepharostoma trichophyllum		10			5		5		10			
Cephalozia lunulifolia	30									70		
Lophozia ventricosa s.l.	10			10					10			
Lepidozia reptans	20	10	4 =	4.0	0			4 =	20			
Ptilidium pulcherrimum		1	15	10	8			15	1	50	100	
Scapania paludicola Cephaloziella elachista											100 100	
Calypogeia sphagnicola	10										90	
Sargpogota opitagittoota	10											

Table 4. Continued

Species				Spe	ecies	freq	uency	y in	habit	ats (	appro	ox.%)
•	FF	BS	AB	BB								SP ED
			M	USCI	-							
Bryum pseudotriquetrum	100			0001	-							
Calliergon cordifolium	100											
Dicranum drummondii	100											
Dicranum polysetum	100											
Hylocomiastrum umbratum	100											
Plagiomnium elli pticum	100											
Plagiomnium medium	100											
Polytrichum strictum	100											
Pseudobryum cinclidioides	100											
Ptilium crista-castrensis	100											
Rhizomnium pseudopunctatum	100											
Rhodobryum roseum	100											
Rhytidiadelphus subpinnatus	100											
Sphagnum (14 species)	100											
Dicranum majus	90	5									5	
Hylocomium splendens	90	5									5	
Straminergon stramineum	90									10		
Warnstorfia fluitans	90							10				
Aulacomnium palustre	85	10			5							
Pleurozium schreberi	85							5			10	
Polytrichum commune	65	35										
Cirri phyllum piliferum	50		50									
Rhizomnium punctatum	50		20							20		
Dicranum scoparium	30	10	15	10						10	25	
Atrichum undulatum		100										
Dicranella cerviculata		100										
Dicranella crispa		100										
Dicranella heteromalla		100										
Ditrichum heteromallum		100										
Ditrichum pusillum		100										
Pogonatum dentatum		100										
Pogonatum urnigerum		100										
Polytrichastrum longisetum		100										
Polytrichastrum pallidisetum		100										
Schistostega pennata		100										
Oligotrichum hercynicum		100										
Pohlia andalusica		100										
Polytrichum juni perinum	10	90										
Ceratodon purpureus		80								10	10	
Pohlia nutans		80									20	
Amlystegium subtile			100									
Campylium chrysophyllum			100									
Fissidens adianthoides			100									
sopterygiopsis pulchella			100									
Plagiomnium cuspidatum			100									
Brachythecium erythrorrhizon	5		80	5				5			5	
Campylium sommerfeltii			70								30	
Eurhynchium pulchellum			70							30		
Rhytidiadelphus triquetrus	30		70									
Brachythecium salebrosum	10		55			5		5	5		20	
Amblystegium serpens		5	50	20							25	
Brachythecium velutinum		5	50	5				5			35	
Callicladium haldanianum				100								
Hypnum pallescens							100					
Pylaisia polyantha									90		10	
Orthotrichum speciosum							15		85			
Orthotrichum obtusifolium			12	25			12		51			

Table 4. Continued.

Species		D.C.	_				y in habi					ED
	FF	BS	AB	BB	SB	РВ	RB WB	AS	BR	RW	SP	ED
Amphidium lapponicum									100			
Andreaea rupestris									100			
Bartramia ithyphylla									100			
Bartramia pomiformis									100			
Bryum flaccidum									100			
Cnestrum schistii									100			
Cynodontium strumiferum									100			
Cynodontium tenellum									100			
Dicranella grevelleana									100			
Dicranum bergeri									100			
Grimmia muehlenbeckii									100			
Hedwigia ciliata									100			
Heterocladium dimorphum									100			
Homalia trichomanoides									100			
Hypnum cupressiforme									100			
Isothecium alopecuroides									100			
Isothecium myosuroides									100			
Kiaeria blyttii									100			
Mnium stellare									100			
Neckera oligocarpa									100			
Paraleucobryum longifolium									100			
Plagiothecium piliferum									100			
Pohlia cruda									100			
Pterigynandrum filiforme									100			
Racomitrium fasciculare									100			
Racomitrium microcarpon									100			
Saelania glaucescens									100			
Schistidium papillosum									100			
Taxi phyllum wissgrillii									100			
Tuxt prigitum &issgritti Timmia austriaca									100			
Tortella tortuosa									100			
Dicranum montanum				15	15				55	15		
Plagiothecium denticulatum				13	30		30		40	13		
Herzogiella turfacea					50		50		40	100		
Oncophorus wahlenbergii										100		
Tetraphis pellucida		10			10					80		
Dicranum fuscescens	10	5		20	5	5			5	50		
•	10		20	20	3	3	10		3			
Sanionia uncinata  Brachuthocium, raflarum	15	10 5	20	5	10		10			50 40		
Brachythecium reflexum		5 5	30	5 5						40		
Brachythecium starkei	10	3	30	J	30 30		20					
Dicranum flagellare					30		30			40		
Plagiothecium curvifolium	10		2	20	30	2	30		1.0	40		
Dicranum flexicaule	16	_	3	20	3	3			16	39		
Brachythecium oedi podium	20	5	30	5	20		-		20	30		
Plagiothecium laetum		20		10	20		5		20	25		400
Splachnum luteum												100
Splachnum rubrum												100
Tetraplodon (2 species)												100

palmata, R. multifida (all near threatened – NT). Moreover, Polytrichastrum pallidisetum, considered as regionally extinct in Finland (RE), have been collected four times in the study area on disturbed soil over roots of fallen trees. This species sporadically occurs in

Russian Karelia (Volkova & Maksimov, 1993) and in Leningrad Province (Kurbatova *et al.*,1999). *Nardia japonica*, recently found as new for Finland (Potemkin, in press), is the other rare species probably of conservation concern.

# COMPARISON WITH THE CENTRAL NORWAY SPRUCE STANDS

Comparison of the studied bryophyte flora with the bryophyte flora of Central Norway spruce stands (Frisvoll, 1997) shows that despite different species number (19 and 28 species erspectively), they have rather common composition of most frequent species. All 22 liverwort species of the studied area found in highest number of studied stands (from 96 to 22% of studied stands) occur in the Central Norway spruce stands. However, studied stands differ from the Central Norway spruce stands in presence of 18 species (positive differential species), which occur less frequently and were found mostly on bared soil and in rocky habitats (Anastrophyllum saxicola, Anthelia juratzkana, Blasia pusilla, Cephaloziella elegans, Cladopodiella francisci, Jungermannia confertissima, J. hyalina, Marsupella sprucei, Nardia insecta, N. japonica, Scapania lingulata) or in swampy conditions (Cephaloziella elachista, Cladopodiella fluitans, Mylia anomala). Moreover, 39 species (negative differential species) were recorded for the Central Norway spruce stands but not found in the North Karelian stands. These species are mainly characteristic for eutrophic and calcareous soils and for regions with  $\pm$  oceanic climate (e.g., Bazzania tricrenata, B. trilobata, Calypogeia azurea, Chiloscyphus coadunatus, Diplophyllum albicans, Frullania tamarisci, Jungermannia exsertifolia, Scapania paludosa). Furthermore, in the studied flora there were not found such species of  $\pm$  arcto-montane distribution as *Barbi*lophozia quadriloba, Lophozia opacifolia, L. sudetica, Odontoschisma elongatum, Tetralophozia setiformis, which are characteristic of the Central Norway spruce stands.

18 moss species of the Norh Karelian flora found in highest number of studied stands (from 100 to 78 % of studied stands) occur in the Central Norway spruce stands. Among species with lower stand frequency there are 36 species which are known from the study area and absent in the Central Norway spruce stands, i.e. positive differential species. They include 6 species growing at base and on bark of aspen (Amblystegium serpens, A. subtile, Brachythecium erythrorrhyzon, Campylium chrysophyllum, C. sommerfeltii, Pylaisia polyantha) and 7 species

of the genus Sphagnum, having apparently more continental distribution (Sphagnum compactum, S. fallax, S. fuscum, S. lindbergii, S. magellanicum, S. riparium, S. wulfianum). Moreover, there is a considerable group of species, which occurrence appears to be possible in the Central Norway spruce stands, but they were not found there (Amphidium lapponicum, Callicladium haldanianum, Calliergon cordifolium, Cnestrum schisti, Dicranum bergeri, D. drummondii, D. flagellare, Ditrichum pusillum, Grimmia muehlenbeckii, Herzogiella turfacea, Heterocladium dimorphum, Hypnum pallescens, Neckera oligocarpa, Plagothecium curvifolium, Pogonatum dentatum, Polytrichastrum pallidisetum, Saelania glaucescens, Splachnum luteum, Taxiphyllum wissgrillii). The studied moss flora is characterized by absence of 106 species (negative differential species), which were recorded in the flora of the Central Norway spruce stands. They include some ± arcto-mountain species (e.g., Blindia acuta, Plagiobryum zieri), many calciphilous and eutrophic species (Amphidium mougeotii, Brachythecium glareosum, Distichium capillaceum, Gymnostomum aeruginosom, Neckera complanata, etc.), some species of suboceanic (e.g., Racomitrium affine, Rhytidiadelphus loreus, Sphagnum rubiginosum) as well as of nemoral distribution (Mnium hornum, Plagiomnium affine, Plagiothecium undulatum, etc.).

Aforementioned distinctions in the species composition of liverworts and mosses result in difference of both floras in taxonomic structure. Species numbers in the leading families and genera in floras of spruce stands of the North Karelian Biosphere Reserve and adjacent territories of Finland and of Central Norway may be represented as follows: Lophoziaceae (19 vs. 25), Jungermanniaceae (9 vs. 9), Cephaloziaceae (8 vs. 4), Scapaniaceae s.str. (6 vs. 11), Geocalycaceae (5 vs. 7), Calypogeiaceae (5 vs. 6); Dicranaceae (19 vs. 24), Sphagnaceae (14 vs. 11), Brachytheciaceae (10 vs. 13), Polytrichaceae (9 vs. 9), Hypnaceae (8 vs. 11), Amblystegiaceae (8 vs. 8), Mniaceae (7 vs. 17), Bryaceae (6 vs. 16); Lophozia (8 vs. 13), Scapania (6 vs. 11), Barbilophozia (6 vs. 7), Cephalozia (6 vs. 4), Calypogeia (5 vs. 6), Jungermannia (4 vs. 7), Sphagnum (14 vs. 11), Dicranum (9 vs. 6), Brachythecium (6 vs. 9), Plagiothecium (4 vs. 8), and *Polytrichum* (3 vs. 5).

Together with distinctions in taxonomic composition of the studied and the Central Norway spruce stands their difference in species frequency and composition of dominant moss species of forest floor is obvious. Some liverwort species (Calypogeia integristi pula, Barbilophozia attenuata, Blepharostoma trichophyllum, Lepidozia reptans, Anastrophyllum minutum, etc.) are more frequent in the studied area than in the Central Norway stands whereas the other (Cephalozia lunulifolia, Barbilophozia lycopodioides, Lophozia obtusa, Barbilophozia barbata, Tritomaria quinquedentata, Barbilophozia floerkei, etc.) are more rare in the studied area, i.e. more frequent in the Central Norway stands. This distinction may result from differences in climate (moderately continental vs. suboceanic), edaphic conditions (soils rather poor vs. rather rich), and landscape (plain vs. mountain). The compared areas have partly similar composition of dominant moss species of the forest floor. However, in the flora of old-growth spruce forests of North Karelia the species of the genus Sphagnum take larger part in forest floor formation whereas suboceanic species of some other genera are absent (Rhytidiadelphus loreus, Plagiothecium undulatum, Polytrichastrum formosum) or very rare (Hylocomiastrum umbratum, Rhytidiadelphus subpinnatus).

# **CONCLUSIONS**

- 1. 119 moss species of 64 genera and 26 families and 75 liverwort species of 29 genera and 19 families were found in 21 fragmented old-growth spruce forest stands of the North Karelian Biosphere Reserve and adjacent territories of Finland. The families of mosses, leading in number of species in the flora, are Dicranaceae (19 species), Sphagnaceae (14), Brachytheciaceae (10), Polytrichaceae (9), Amblystegiaceae (8), Hypnaceae (8), Mniaceae (7), Bryaceae (6), Hylocomiaceae (5) and Plagiotheciaceae (4 species). The families of liverworts, leading in number of species in the flora, are Lophoziaceae (19 species), Jungermanniaceae (9), Cephaloziaceae (8), Scapaniaceae (6), Geocalycaceae (5) and Calypogeiaceae (5 species).
- 2. Among 21 studied old-growth spruce forest stands, the highest number of species have *Haapahaasianvaara* (63 species), *Raiskionaho* (66), *Salmivaara* (62), *Syväjärvi* (68), *Ukonsärkkä* (66), and particularly *Pieni Kotavaara*

- (91) and *Pampalo* (140). The species diversity of the studied stands is predetermined by degree of their microhabitat diversity, which closely correlates first of all with their moisture, presence of aspen, constantly shaded rocks and amount of rotten wood. The number of species in the studied stands is not correlated with their area.
- 3. Most common moss species in old-growth spruce stands of the North Karelian Biosphere Reserve and adjacent territories of Finland, which have mainly a dominant role in the forest floor formation, are Pleurozium schreberi, Hylocomium splendens, Dicranum scoparium, D. majus, D. polysetum, Sphagnum angustifolium, S. girgensohnii, S. russowii, Polytrichum commune. The most common liverwort species are Ptilidium pulcherrimum, Calypogeia integristipula, Barbilophozia attenuata, Blepharostoma trichophyllum, Lophozia ventricosa s.l., Lophozia longiflora, Lophozia longidens, Barbilophozia lycopodioides, Cephalozia lunulifolia, Lepidozia reptans. They were collected in most studied stands and have higher total frequency in comparison with the other species of the flora.
- 4. Liverworts and mosses have different ecological distribution in the studied area. Species diversity of liverworts is considerably higher on rotten wood and bare soil whereas the species diversity of mosses is higher on rocks and at bases and bark of deciduous trees. This appears to be resulted from stronger ability of liverworts than mosses to inhabit wet old logs characteristic of old-growth spruce forests and from weak ability of liverworts to grow on drier rocks, boulders, bases and bark of deciduous trees.
- 5. Nine bryophyte species (Anastrophyllum hellerianum, Calypogeia suecica, Cephalozia macounii, Harpanthus scutatus, Herzogiella turfacea, Lophozia ascendens, Polytrichum pallidisetum, Riccardia multifida, R. palmata) included in Red Data Book of Finland (Rassi & al., 2001) have been revealed in the North Karelian Biosphere Reserve and adjacent territories of Finland. They occur on rotten wood and bared soil in the area under research.
- 6. The bryophyte flora of fragmented oldgrowth spruce forest stands of the North Karelian Biosphere Reserve and adjacent areas of Finland is characterized in comparison with the flora of the Central Norway spruce stands by 54 positive differential species (36 mosses and 18 hepatics)

and 145 negative differential species (39 hepatics and 106 mosses). It has more poor representation of the most families and genera leading in number of species, except family Sphagnaceae and genus Sphagnum. Specificity of the taxonomic composition of the flora is predetermined by moderately continental climate, absence of euthrophic and calcareous soils, presence of spruce forest of Myrtillus type with often admixture of aspen, plain relief of the territory, and restricted occurrence of rocky outcrops.

# **ACKNOWLEDGEMENTS**

The project was financially supported by Finnish Ministry of the Environment, Metsähallitus and Regional Environment Centre of North Karelia. Diverse assistance of administration and staff of the North Karelian Biosphere Reserve and Mekrijärvi Research Station, Ilomantsi, during our work on the project is kindly acknowledged. We are obliged to Dr. Vera M. Kotkova (V.L. Komarov Botanical Institute, St. Petersburg, Russia) for careful reading of the manuscript, valuable corrections and helpful discussion. Dr. Svetlana I. Grabovik (Institute of Biology; Petrozavodsk, Russia) is thanked for help in field work in 1996-1997. We are grateful to Dr. Sanna Laaka-Lindberg (Lammi biological station, Finland) and the anonymous rewiever for important comments on the first version of the manuscript.

# LITERATURE CITED

- AHTI, T., L. HAMET-AHTI & J. JALAS 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fennici* 5: 169-211.
- CAJANDER, A. K. 1926. The theory of forest types. *Acta Forest. Fennica* **29**(3): 1-108.
- FRISVOLL, A. A. 1997. Bryophytes of spruce forest stands in Central Norway. *Lindbergia* **22**(2): 83-97.
- FRISVOLL, A. A. & T. PRESTÖ 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. – Ecography 20: 3-18.
- GROLLE, R. & D. G. LONG 2000. An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. *J. Bryol.* **22**: 103-140.
- GUSTAFSSON, L. & T. HALLINGBÄCK 1988. Bryophyte flora and vegetation of managed and virgin coniferous forest in south-west Sweden. – *Biol. Conserv.* 44: 283-300.
- HALLINGBÄCK, T. 1991. Mossor som indikerar skyddsvard skog. Svensk. Bot. Tidskr. 81: 321-332.
- HELMINEN, J. (ed.) 1997. Ilmastokatsaus-lehti 1-12. Ilmatieteen laitos, Helsinki.
- ENGEL J. J. & R. M. SCHUSTER 1984. An overview and evaluation of the genera of Geocalycaceae. Subfamily Lophocoleoideae (Hepaticae) – Nova Hedwigia 39: 385-463.
- IGNATOV, M. S. & O. M. AFONINA (eds.) 1992. Check-list of mosses of the former USSR. *Arctoa* 1(1-2): 1-85.
- [KURBATOVA, L. E., G. YA. DOROSHINA-UKRAIN-SKAYA & E. O. KUZMINA] КУРБАТОВА Л. Е., Г. Я. ДОРОШИНА-УКРАИНСКАЯ, Е. О. КУЗЬМИНА 1999. Листостебльные мхи Ленинградской области — [Mosses of the Leningrad Region] В кн.: Балашова Н. В., А. А. Заварзин (ред.) Биоразнообразие Ленинградской области. Тр. СПб общ. естествоиспытателей.

- СПб. Сер. **6**, 2 [In: Balashova, N. B. & A. A. Zavarzin (eds.) Biodiversity of the Leningrad Region. Trudy Sankt-Peterburgskogo Obshchestva Estestvoispytateley. St. Petersburg. Ser. **6**, 2]: 271-302.
- POTEMKIN, A. D. 1999. Circumscription of the family Scapaniaceae with segregation of the new family Diplophyllaceae (Hepaticae). – Ann. Bot. Fennici 36: 271-283.
- POTEMKIN, A. D. (in press) Rare and new for Finland and Karelia borealis hepatics from the North Karelia Biosphere Reserve and adjacent territories *Mem. Soc. Sci. Flora Fauna Fennica*.
- RASSI, P., A. ALANEN, T. KANERVA & I. MANNERKOSKI (eds.) 2001. Suomen lajien uhanalaisus 2000. Ympäristöminesteriö & Suomen ymparistökeskus, Helsinki.
- SÖDERSTRÖM, L. 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in northeast Sweden. *Biol. Conserv.* **45**: *169-178*.
- SÖDERSTRÖM, L. (ed.) 1996. Preliminary distribution maps of bryophythes in northwestern Europe. 2. Musci (A-I). *Mossornas Vännar, Trondheim. 72 pp.*
- SÖDERSTRÖM, L. (ed.) 1998. Preliminary distribution maps of bryophythes in northwestern Europe. 3. Musci (J-Z). Mossornas Vännar, Trondheim. 69 pp.
- UNESCO 2002. Biosphere Reserves: Special places for people and nature. UNESCO, Paris. 208 pp.
- [VOLKOVA, L. A. & MAKSIMOV, A. I.] ВОЛКОВА Л. А. и МАКСИМОВ А. И. 1993. Список листостебельных мхов Карелии. [List of mosses of Karelia] В кн.: Елина Г. А., А. Д. Волков (ред.) Растительный мир Карелии и проблемы его охраны. Петрозаводск. [In: Elina, G. A. & A. D. Volkov (eds.), Rastitel'ny mir Karelii i problemy ego okhrany. Petrozavodsk]: 173-194.