Patterns of epixylic vegetation on spruce logs in late-successional boreal forests

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Abstract

There is a wide diversity in composition and structure of epixylic vegetation that depends on the stage of overgrowing, species of logs, ecological conditions, geographical position and random factors. We analyzed vegetation on spruce logs in the late successional spruce forests of the *Sphagnum–Myrtillus*, *Myrtillus* and *Oxalis* types in northwestern Russia.

Vascular plants, lichens, hepatics and mosses constitute, respectively, 18, 17, 21 and 44% of the flora on the decaying wood. The total number of species increases from the first to the second stage of overgrowing, and then decreases at the fourth stage. However, the number of species per plot barely changes. The dynamics of epixylic species and generalists depend on the phytosociological conditions.

The described sequences of vegetation are divided into three types of microsuccession. The first type is characterized by the dominance of the epiphytes in the early stages and the epigeous species in the late stages. The low abundance of generalists and epixylics is observed in the spruce forests with well-developed ground feather moss cover. The second type of microsuccession has a small coverage and number of epigeous species and a significant share of generalists on the latter stages of overgrowing. It is connected with the herb-rich, mainly deciduous forests. The third type of microsuccession includes one more stage where one group of ground flora mosses (green mosses) is replaced with another one (*Sphagnum*). This is characteristic for the *Sphagnum–Myrtillus* type of spruce forests.

1. Introduction

The single uprootings, cohort replacing and/or stand replacing windthrows are characteristic for natural forest ecosystems. A set of ecological substrata – soil–windfall complexes of different sizes and ages – is formed. Intensive forest management treatment – especially regular thinning of stands, clear cut harvesting, efficient forest fire prevention, usage of dead wood for construction and fire-wood, the threat of insect pests and salvation logging after natural disturbances – have all contributed to the loss of habitats and the transformation of remaining habitats into homogenous and productive structures. The total amount of coarse woody debris (CWD), the structural diversity of CWD, the share of leaning trees and natural stumps, dramatic reductions of large fallen trees in late stages of decay all contribute to soil–windfall

complexes being almost absent (Berg et al., 1994; Kruys et al., 1999; Shorohova and Tetioukhin, 2004). This causes a general decrease of biodiversity in managed forests (cf. Angelstam et al., 2004).

During the last decades the epixylic cryptogam communities and some general features of their dynamics have been described in different regions of Temperate Belt (Harmon, 1989; McAlister, 1997; Rambo and Muir, 1998; Södeström, 1988b). The studies of overgrowing of the soil–windfall complexes' elements, mainly pits and mounds, in the pristine Norway spruce forests of the southern (Skvortsova et al., 1983; Bobrov et al., 2002) and northern (Jonsson and Esseen, 1990, 1998) boreal zone showed significant variability of structure and composition of plant microgroups. The heterogeneity of bryophyte groups established on the CWD of first decay stage is enhanced by the heterogeneity of decay stages within one fallen tree (Pyle and Brown, 1999).

To help classify the huge complexity of ecosystems of decaying wood from a dynamic perspective, the stages of microsuccessions were distinguished and described (McCullough, 1948; McAlister, 1997; Södeström, 1988b). It was

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shown that the structure and composition of bryophyte groups are connected to the characteristics of decaying wood viz.: species, decay stage, bark cover, pH as well as wood density and texture (McCullough, 1948; Andersson and Hytteborn, 1991; Södeström, 1988b; McAlister, 1997).

The tendencies of substrate specificity of epixylic species (Kruys et al., 1999) and dynamics of some ecological groups (Södeström, 1988b; Andersson and Hytteborn, 1991) were investigated in intensively managed forests with low availability of CWD. The analysis of the bryophyte flora indicated different composition of hepatics in the managed and semi-natural forests, whereas the abundance of feather mosses depended on other factors including substrate availability (Gustaffson and Hallingbäck, 1988; Södeström, 1988b; Andersson and Hytteborn, 1991). The populations of some xylophilous mosses were influenced by the distance between the available substrata, i.e. habitat fragmentation played a noticeable role (Herben and Södeström, 1992).

To elicit the factors driving forest vegetation diversity it is necessary to compare the structure and composition of plant microgroups connected with the soil–windfall complexes in managed and semi-natural forests. There is insufficient data on the impact of both substrate features and ecosystem-level ecological factors (i.e. climatic factors, site conditions and phytosociological factors) on the epixylic microsuccessions.

This study aims to reveal the dependence of both structure and composition of epixylic vegetation on Norway spruce fallen logs on forest type in late-successional boreal forests. We hypothesized that site conditions and ground vegetation are affecting the microsuccessional pathways. The specific objectives were defined as: (i) inventory of the epixylic flora in several forest types, (ii) description of the stages of microsuccession in terms of share of different ecological groups and species diversity, and (iii) revealing the differences in the microsuccessional pathways.

2. Materials and methods

The data were collected from eight study plots located in the Leningrad region, Russia. The Leningrad region is situated in the northeastern part of the Eastern-European plain. The territory represents mainly a hilly plain with a well-developed hydrological network. The bedrock consists of glacial quaternary deposits of different mechanical composition. The climate is sub-oceanic with southwestern winds prevailing. The total annual precipitation averages 600 mm, and varies from 400 to 900 mm. The annual temperature averages $+2\,^{\circ}$C. The frost-free period lasts 115–130 days. The total number of days with temperatures greater than $0\,^{\circ}$C in the studied area constitutes 211–222 days, and temperatures greater than $10\,^{\circ}$C, 165–175 days. The sum of active temperatures (greater than $10\,^{\circ}$C) varies from 1600° to 1700°, reaching 1800° in the southern part of the region. The precipitation during the growing season is 275–300 mm. The hydrothermic coefficient equals 1.6–1.7.

Seasonal snow cover usually appears at the end of November and the beginning of December, only a month after of the

Table 1
Characteristics of the sites

Site	Coordinates	Sample size[a]	Stand composition	Shrub layer	Dominants of the moss–lichen layer	Dominants of the herb-dwarf-shrub layer
K	60°35′N, 30°16′E	50	*Picea abies* 90%, *Pinus sylvestris* 10%	*Sorbus aucuparia*	*Pleurozium schreberi*	*Avenella flexuosa*, *Vaccinium myrtillus*, *Maianthemum bifolium*
L1	58°52′N, 29°47′E	45	*P. abies* 90%, *P. sylvestris* 10%	*Lonicera xylosteum*, *Ribes alpinum*, *S. aucuparia*, *Rubus idaeus*	*P. schreberi*, *Hylocomium splendens*, *Plagiomnium affine*	*Oxalis acetosella*, *Galeobdolon luteum*, *Hepatica nobilis*
L2	59°04′N, 29°38′E	25	*P. abies* 50%, *Populus tremula* 40%, *Alnus incana* 10%	*R. alpinum*, *S. aucuparia*		*O. acetosella*, *Maiantemum bifolium*, *Pulmonaria obscura*, *Stellaria holostea*, *Asarum europaeum*
L3	59°04′N, 29°38′E	27	*P. abies* 70%, *P. tremula* 30%	*S. aucuparia*	*P. schreberi*, *H. splendens*, *Sphagnum girgensohnii*	*V. myrtillus*, *O. acetosella*, *Vaccinium vitis-idaea*
V1	60°01′N, 34°43′E	22	*P. abies* 70%, *Betula pubescens* 10%, *P. tremula* 5%, *A. incana* 5%	*S. aucuparia*	*H. splendens*, *P. schreberi*, *Dicranum polysetum*	*O. acetosella*, *Dryopteris carthusiana*, *V. myrtillus*, *V. vitis-idaea*, *Rubus saxatilis*
V2	60°12′N, 34°54′E	32	*P. abies* 100%	*S. aucuparia*	*D. polysetum*, *P. schreberi*, *S. girgensohnii*	*V. myrtillus*, *V.vitis-idaea*, *M. bifolium*, *Linnaea borealis*, in some patches *O. acetosella*, *Dryopteris expansa*
V3	60°12′N, 34°54′E	17	*P. abies* 90%, *B. pubescens* 10%	*S. aucuparia*	*P. schreberi*, *S. girgensohnii*, *D. polysetum*, *Ptilium crista-castrensis*, *Plagiochila porrelloides*	*V. myrtillus*, *V.vitis-idaea*, *D. expansa*
V4	60°12′N, 34°54′E	51	*P. abies* 90%, *B. pubescens* 10%	*S. aucuparia*	*S. girgensohnii*, *Sphagnum magellanicum*, *Sphagnum* spp., *Polytrichum commune*	*V. myrtillus*, *V.vitis-idaea*, *Rubus chamaemorus*

[a] Number of plots for descriptions of epixylic vegetation.

Table 2
The substrate specificity, frequency and coverage (in percent of wood substrate) of the species of bryophytes and lichens

Species	Substrate specificity	Frequency	C	S.E. (C)
P. schreberi	epg	0.88	27.99	2.05
Ptilidium pulcherrimum	epf	0.57	12.53	1.29
Dicranum scoparium	epg	0.41	3.71	0.62
D. polysetum	epg	0.38	3.66	0.57
Saniona uncinata	g	0.31	2.45	0.60
Lophocolea heterophylla	epx	0.29	2.09	0.54
H. splendens	epg	0.27	4.95	0.89
Plagiothecium laetum	g	0.19	0.58	0.27
Cladonia coniocraea	g	0.17	2.00	0.48
Cladonia sp.	epg	0.15	0.69	0.23
P. crista-castrensis	epg	0.13	0.76	0.38
Brachythecium starkei	g	0.10	1.47	0.56
S. magellanicum	epg	0.08	1.50	0.56
Hypnum cupressiforme	g	0.07	1.16	0.40
Sphagnum sect. Acutifolia	epg	0.07	1.19	0.42
Hypogymnia physodes	epf	0.07	0.24	0.11
Pohlia nutans	g	0.07	0.10	0.03
Vulpicida pinastri	epf	0.07	0.14	0.05
Herzogiella seligerii	epx	0.06	0.31	0.15
Brachythecium oedipodium	g	0.05	0.31	0.18
Tetraphis pellucida	epx	0.05	0.22	0.14
Dicranella heteromalla	epg	0.05	0.23	0.10
Orthodicranum montanum	epf	0.05	0.04	0.01
Orthocaulis attenuatus	epg	0.05	0.15	0.06
P. affine	g	0.04	0.80	0.36
Rhythidiadelphus triquetrus	epg	0.04	0.22	0.20
S. girgensohnii	epg	0.04	0.67	0.36
Pylasiella polyantha	epf	0.04	0.08	0.05
Calypogeia integristipula	g	0.03	0.17	0.12
Blepharostoma trichophyllum	epx	0.03	0.04	0.02
Cephalozia lunulifolia	g	0.03	0.03	0.02
Cladonia cornuta	epg	0.03	0.07	0.03
Dicranum fuscescens	g	0.03	0.25	0.14
Plagiomnium cuspidatum	g	0.02	0.03	0.02
Brachythecium reflexum	g	0.02	0.35	0.23
Calypogeia muelleriana	g	0.02	0.11	0.07
Cladonia rangiferina	epg	0.02	0.02	0.01
Dicranum congestum	epg	0.02	0.38	0.22
Cephalozia bicuspidata	epx	0.02	0.03	0.02
Lophozia longidens	epx	0.02	0.07	0.06
Parmeliopsis ambigua	epf	0.02	0.03	0.01
Brachythecium plumosum	g	0.02	0.02	0.02
Brachythecium salebrosum	g	0.02	0.02	0.01
Lophozia ventricosa	epx	0.02	0.07	0.05
Parmelia sulcata	epf	0.02	0.05	0.03
Brachythecium populeum	g	0.01	0.09	0.08
Bryum sp.	g	0.01	0.01	<0.01
Cladonia arbuscula	epg	0.01	0.02	0.01
Calypogeia sphagnicola	epg	0.01	0.02	0.01
Lophozia longiflora	epx	0.01	<0.01	<0.01
Radula complanata	epf	0.01	0.01	<0.01
Xanthoria sp.	epf	0.01	0.01	<0.01
Plagiothecium denticulatum	g	0.01	0.21	0.20
Amblystegium serpens	g	0.01	0.01	<0.01
Campylium chrysophyllum	g	0.01	<0.01	<0.01
Cephaloziella divaricata	g	0.01	<0.01	<0.01
Chyloscyphus sp.	g	0.01	0.01	0.01
Cladonia pityrea	epg	0.01	0.06	0.06
Plagiochila asplenioides	epg	0.01	0.03	0.02
Dicranum majus	epg	0.01	0.28	0.22
Polytrichum juniperinum	epg	0.01	0.09	0.08
Polytrichum strictum	epg	0.01	0.04	0.03

Table 2 (Continued)

Species	Substrate specificity	Frequency	C	S.E. (C)
Brachythecium velutinum	epx	0.01	<0.01	<0.01
Dicranum fragilifolium	epx	0.01	<0.01	<0.01
Jamsoniella autumnalis	epx	0.01	<0.01	<0.01
Lepidozia reptans	epx	0.01	0.03	0.02
Platydictya subtilis	epx	0.01	<0.01	<0.01
Novellia curvifolia	epx	0.01	0.01	0.01
Parmeliopsis hyperopta	epf	0.01	0.01	0.01
Usnea sp.	epf	0.01	<0.01	<0.01

Substrate groups: epf, epiphytic; epg, epigeous; epx, epixylics; g, generalists. C, mean coverage; S.E. (C), standard error of mean coverage ($P < 0.05$).

establishment of negative air temperatures. Despite stronger frosts in the eastern part of the region, accumulated snow cover delays freezing of the soil. Therefore, soil freezing is approximately the same in both the western and eastern parts, averaging 40–50 cm. In some winters, it is more than 100 cm.

The studied territory belongs to the middle and southern taiga zones (Vegetation, 1980). The spruce forests of *Oxalis* type in combination with spruce forests of *Myrtillus* type and small patches of the nemoral herb-rich spruce forests normally prevail on the plains. The *Myrtillus* spruce forests represent the zonal middle taiga types. The *Calamagrostis–Myrtillus* spruce forests – where *Calamagrostis arundinacea*, *Convallaria majalis*, *Rubus saxatilis*, *Pteridium aquilinum* are abundant along with *Vaccinium myrtillus* – are also typical.

The study sites were established in mature and over-mature Norway spruce dominated forests of the *Myrtillus*, *Sphagnum–Myrtillus* and *Oxalis* types. More details on the stands are given in Table 1. All the stands had a natural origin and were either never commercially harvested (sites V2–V4) or grew without any management (other sites). The CWD of different species, position and decay stages were available. The proportion of the tree species was calculated using relascope sampling. The plots for the description of epixylic vegetation were established on fallen logs with a diameter at 1.3 m length of not less than 12 cm; 1–3 plots per every log along a transect through site. The length of plots was 50 cm, the width fitted to the diameter of a log. We recorded the position of a plot on a log (tree base, middle part or top), the diameter and height of a tree. The decay stage of wood according to Renvall and Niemelä (1994) was determined for each plot. Describing vegetation on the plots, we estimated the projective cover of mosses, liverworts, lichens and vascular plants. Complicated specimens were collected and identified in the lab.

The stages of dynamics of decaying logs were described (Muhle and LeBlanc, 1975) as: (1) the invasion phase or the hidden stage; (2) the early phase or the incipient stage; (3) the typical phase or the advanced stage; (4) the final stage. We modified this classification by using the features of epixylic vegetation as a baseline for arranging the stages of microsuccessions as overgrowing of decaying wood. The system used is described. The earliest first stage is characterized by a sparse vegetation cover. It is undoubtedly the primary stage because the decrease of projective cover and thinning of the clumps in the bryophyte-lichen microgroups is scarcely

Table 3
The frequency and mean coverage (in percent of wood substrate) of the vascular species occurred on the dead wood

Species	Frequency	C	S.E. (C)
V. myrtillus	0.15	1.36	0.32
O. acetosella	0.15	1.46	0.32
V. vitis-idaea	0.14	0.90	0.21
L. borealis	0.08	0.90	0.21
Carex globularis	0.07	0.26	0.08
Trientalis europaea	0.07	0.16	0.05
A. flexuosa	0.05	0.10	0.04
M. bifolium	0.04	0.10	0.05
Lycopodium annotinum	0.02	0.22	0.13
R. chamaemorus	0.02	0.13	0.07
Luzula pilosa	0.02	0.03	0.01
Carex digitata	0.02	0.06	0.04
G. luteum	0.02	0.03	0.02
Orthilia secunda	0.01	0.04	0.03
R. saxatilis	0.01	0.04	0.04
Calamagrostis arundinacea	0.01	0.02	0.02
D. expansa	0.01	0.02	0.02
Gymnocarpium dryopteris	0.01	0.01	<0.01
Fragaria vesca	<0.01	0.04	0.04
H. nobilis	<0.01	<0.01	<0.01
R. idaeus	<0.01	<0.01	<0.01
D. carthusiana	<0.01	<0.01	<0.01

C, mean coverage; S.E. (C), standard error of mean coverage ($P < 0.05$).

possible. The closed groups with cover of not less than 70% formed by mainly non-epigeous species were treated as the second stage. The plots with the dominance of ground cryptogam species without significant contribution of vascular plants were considered as the third stage. The overgrowing of wood is completed by establishment and spread of vascular plants, which indicated the fourth stage.

Andersson and Hytteborn (1991) classified the bryophyte species by substrate specificity. In cases of absence of the species in the above paper we used the published flora check-lists (Ignatov and Ignatova, 2003, 2004; Schljakov, 1976, 1979, 1980, 1981, 1982) as well as our observations of substrate preferences of the species. The vascular plants were considered separately. The following classification was acquired. All cryptogam species were divided into four groups: epiphytes – growing mainly on the stems of living trees, epixylics – using dead wood as on the main substrate, epigeous species – forming the ground moss cover in boreal forests, generalists – frequently

occurring on different substrata (Table 2). The abundance and frequency of vascular plants is given in the Table 3.

The Shannon index (H) was calculated by the formula (Magurran, 1988):

$$H = -\sum_{i=1}^{N} S_i \ln S_i \tag{1}$$

where S_i is the part of the ith species in the total cover of the layer and N is the total number of the species on the plot. The Pielou index depicting evenness was calculated as:

$$E = \frac{H}{H_{\max}}, \quad H_{\max} = \ln N \tag{2}$$

As the data did not fit the requirements of parametric methods, the Kruskal–Wallis non-parametric median test was used to compare the substrate groups by stages for different sites. The means and S.D. of projective covers of the substrate groups on different sites were analyzed to explore the vegetation homogeneity of the stages of microsuccessions by the Dunkan test for homogeneity.

Nomenclature for mosses: Ignatov and Afonina (1992), hepatics: Konstantinova et al. (1992), lichens: Santesson et al. (2004).

3. Results

one hundred and twenty-three plants and lichen species were identified on the decaying spruce logs. The 23 species of vascular plants, 53 species of leafy mosses, 26 species of liverworts and 21 species of lichens formed the composition of epixylic vegetation of the study plots. All sites were characterized by a high number of species having both low frequency (1–2 occurrences) and an insignificant part in the epixylic communities. Only bryophyte and lichen species with a frequency greater than 1% are listed (Table 2). Taking into consideration the low abundance of most species, an analysis of the dynamics of all species is not within the scope of this paper. The stages of microsuccessions are generally described in the Table 4.

Thirty-six species were found in the microgroups of the first stage of a substrate overgrowing. Five species (*Cladonia* spp., *Dicranum scoparium*, *Pleurozium schreberi*, *Ptilidium pulcherrimum*, *Sanionia uncinata*) were the most abundant. In all studied communities *P. pulcherrimum* – the facultative epiphyte,

Table 4
Characteristics of the stages of microsuccession

	Stages of microsuccession			
	1	2	3	4
Total number of species of bryophytes and lichens	36	73	62	54
Average number of species of bryophytes and lichens per plot	5.1	5.9	5.8	4.6
Standard error of average number of species of bryophytes and lichens per plot	0.39	0.24	0.40	0.38
Total number of species of vascular plants	0	5	5	20
Average number of species of vascular plants	0	0.1	0.3	2.7
Standard error of average number of species of vascular plants per plot	0	0.03	0.07	0.22
Shannon index	1.07	0.97	0.81	0.79
Pielou index	0.68	0.56	0.50	0.52

growing both on the bark of living trees and on decaying wood – was dominant. The co-dominants in poor and dry sites (site K) were epiphytic lichens *Hypogymnia physodes*, *Parmelia sulcata*, *Vulpicida pinastri* and the less abundant *Parmeliopsis ambigua*, *P. hyperopta*, *Usnea glabrata*, *Xanthoria* sp. In the more southern communities (sites L1, L2) there were microgroups with significant parts of *Lophocolea heterophylla* and *S. uncinata*. The typically epigeous species *Cladonia* spp., *Dicranum polysetum*, *D. scoparium*, *P. schreberi*, and the more rare *Hylocomium splendens* and *Rhytidiadelphus triquetrus*

colonized the dead wood from the first stage, having low covers and high frequency.

Three types of composition of epixylic microgroups are distinguished on the first stage in terms of proportion of different substrate groups (Fig. 1). The first type: the epiphytes occupy the dominant position; the role of other groups is not significant. The second type – the share of epiphytes and epigeous species – is approximately equal. The third type was noted only once on the site L1: on the first stage epiphytes and epixylics co-dominate owing to high covers of *L. heterophylla*.
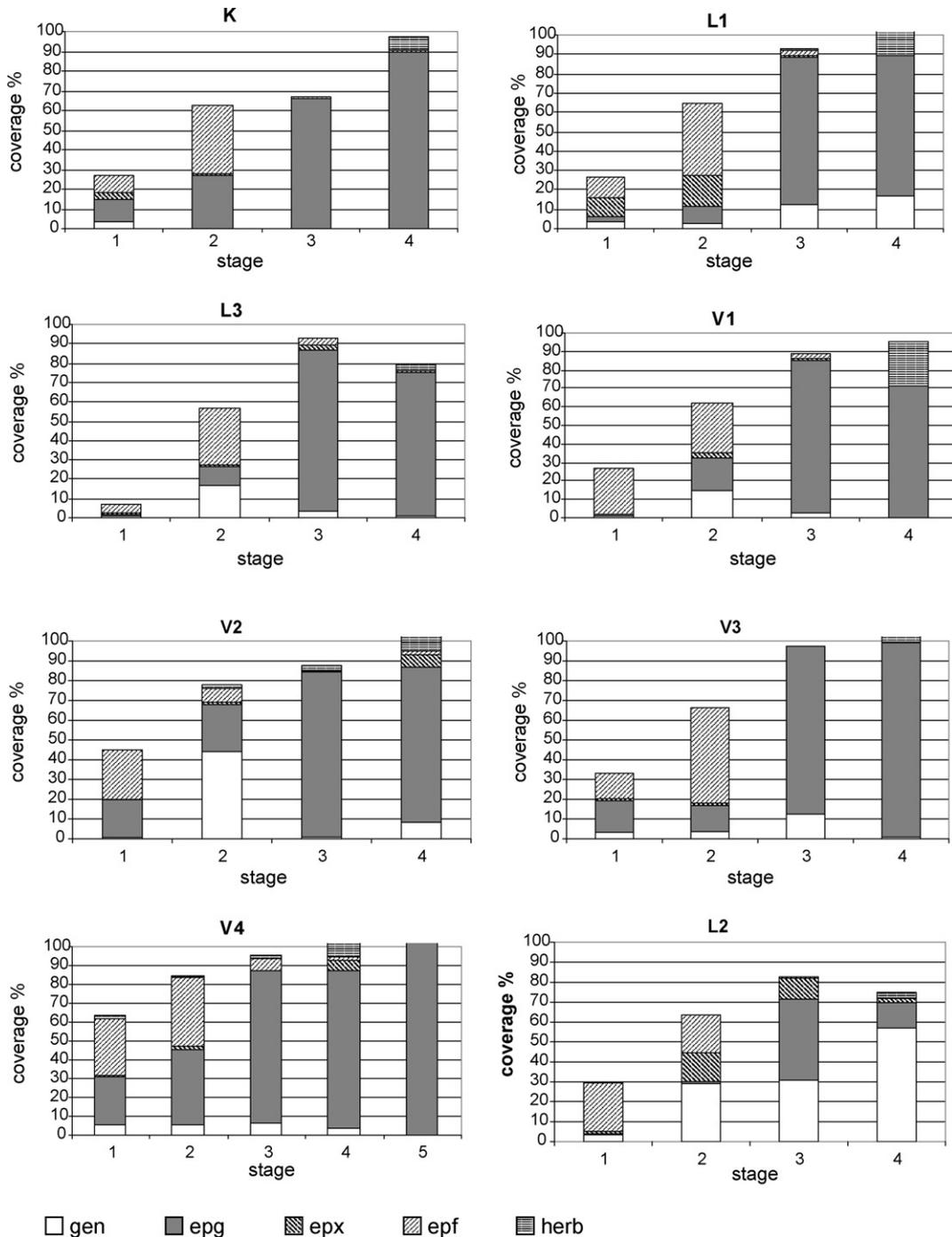

Fig. 1. Dynamics of the substrate groups during overgrowing of the fallen logs on the study plots: epf, epiphytes; epx, epixylics; epg, epigeous species; gen, generalists; herb, vascular plants.

The vegetation cover of the *second stage* is formed by the spread of species that were established during the first stage as well as by active colonization of new species. This stage is the most species rich. Seventy five species were found in total. The species number of all groups increased (Table 4). The increase in share of generalists and epigeous species was more pronounced—14 new species each; only 1 species was added to the list of epiphytes. The number of species characteristic for most communities increased as well. The ground flora mosses *D. polysetum* and *H. splendens* and a generalist *Brachythecium starkei* are added to the five most abundant species of the first stage. *P. pulcherrimum* still keeps the dominant position in the most epixylic microgroups. This moss occupies large areas of the second stage as well due to its active spread (each clump of *P. pulcherrimum* can occupy a few square decimetres, and its average annual growth constitutes 30% of the clump area (Jonsson, 1987)). One of the studied Norway spruce forests (V2) represented an exception from the general trend: *P. pulcherrimum* cedes to two generalists—*S. uncinata* and *B. starkei*. These two mosses occurred in all plant communities during the second stage, but anywhere else their abundance did not reach such high values.

P. schreberi slightly increased its participation; it was a constant and abundant component of the microgroups of the second stage. Its mean cover increased from 2.6% to 4.1% ($\chi^2 = 4.21$, $P = 0.4$). The important change occurs during the second stage: the ground flora species *D. polysetum* and *H. splendens* became more constant components of epixylic microgroups. *D. scoparium* considerably spreads: it is abundant in 5 of the 7 sites. The decrease in abundance, in comparison with the first stage, was observed only for epiphytic lichens on the sites where they were abundant.

During the second stage the epiphytes dominated in all study areas, sometimes with significant parts of generalists (sites L2, L3, V1, V2). The epigeous species increased their cover except of the site L2 (Fig. 2).

The total number of species slightly decreases during the *third stage*. The species list in most communities is approximately the same. *B. starkei* is replaced with *Plagiothecium laetum*, which actively forms specific microgroups on the lateral slopes of the fallen trees. *P. schreberi* dominates on this stage, the co-dominants are *H. splendens* and *D. polysetum*. *P. pulcherrimum* still occurs in most communities, but its abundance is considerably reduced ($\chi^2 = 55.08$, $P < 0.01$). *S. uncinata*, *D. scoparium* and *L. heterophylla* have similar tendencies.

On the all sites except L2 the ratio of substrate groups abruptly changes: the epigeous species dominate, other groups are low in abundance, though the number of species is almost the same (Fig. 2). The epiphytes represent the only group showing a significant reduction in the number of species (Fig. 1).

The outward *fourth stage* of epixylic vegetation best approximates the ground cover. The moss–lichen layer becomes scanty: only 54 species were found. The species number decreases the most (Table 4). The same feather mosses dominate, but the ratio of their abundance changes. Of the 22
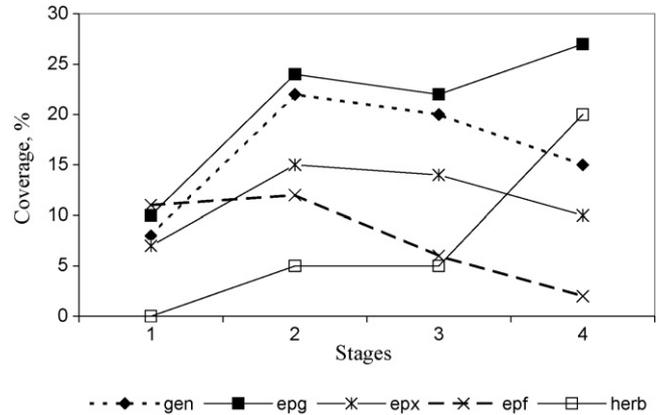

Fig. 2. Dynamics of the substrate groups: epf, epiphytes; epx, epixylics; epg, epigeous species; gen, generalists; herb, vascular plants. See Table 1 for description of the sites.

vascular species only three – the most typical for the studied forest types (*Oxalis acetosella*, *V. myrtillus* and *Vaccinium vitis-idaea*) – were found in all communities.

Fig. 1 shows the ratios of abundance of different substrate groups during the overgrowing processes in all stages. On most sites the patterns of microsuccession are similar. The abundance of generalists during the second–third stages is the most variable characteristic. Most deviations are of a sporadic nature. Only on the site L2 are the deviations from the general scheme constant and directed (post hoc Duncan's test shows significant difference of this site from all others: on the third stage by epixylics, on the fourth stage by dominant generalists and epigeous species, $P = 0.05$). The differences are evident from the second stage onwards. In comparison with other sites, the generalists are more abundant in the microgroups. The ground flora species are less abundant. These differences are so strong that even at the time of colonization by vascular plants the epigeous species on the decaying wood do not become dominant. In contrast, they decrease and cede their place to the generalists.

The results of the Kruskal–Wallis test show the difference by stages in the abundance of different substrate groups on different sites (Table 5). But these results do not separate the set of sites into groups. Checking the significance of the above differences confirmed that only on the site L2 is the abundance of generalists significantly higher and the abundance of epigeous species significantly lower during the stages 2–4. The microgroups of the 2–3 stages on the given site consisted of significantly more epixylics compared with the majority of other sites. Only three epigeous species (*P. schreberi*, *D. scoparium*, *R. triquetrus*) were found in the epixylic microgroups of the fourth stage.

The typical ground flora species abundant during the last stage in other sites, i.e. *D. polysetum*, *H. splendens*, *Ptilium crista-castrensis*, *Plagiomnium cuspidatum*, had few occurrences only during the third stage on the site V4. The species dynamics during the latter stages is different as well. The dynamics of substrate groups follows the general scheme, but analysis of the species composition of the latter stages revealed

Table 5
Results of the Kruskal–Wallis test comparing the coverage of different substrate groups by stages of microsuccession between sites (d.f. = 8)

	Stages of microsuccession							
	1		2		3		4	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P
GEN	5.18	0.739	**45.26**	**<0.001**	**17.97**	**0.021**	**19.77**	**0.011**
EPG	**23.37**	**0.003**	**43.05**	**<0.001**	9.91	0.271	**20.43**	**0.009**
EPX	13.03	0.111	**28.84**	**<0.001**	**19.77**	**0.011**	**29.23**	**<0.001**
EPF	**15.97**	**0.043**	15.25	0.054	**17.77**	**0.023**	8.31	0.404
HERB	11.67	0.167	**15.94**	**0.043**	9.80	0.279	**30.91**	**<0.001**

Substrate groups: epf, epiphytic; epg, epigeous; epx, epixylics; gen, generalists. Significant difference ($P < 0.05$) are boldfaced.

interesting characteristics that were not recorded on other sites. The large feather mosses (*P. schreberi*, *D. polysetum*) absent on the ground form the continuous cover on the decaying wood. These mosses are subsequently replaced by the dominants of the ground cover *Sphagnum magellanicum*, and *S. sect. Acutifolia*. The lichen *Cladonia coniocraea* is quite abundant during the 1–4 stages (relative cover is ca. 10%) and absent at the end of the fourth stage. The maximum abundance of typical epixylics (*Tetraphis pellucida*, *L. heterophylla*, *Lophozia* spp. and other) was registered on the fourth stage only on this site, but at the end of the fourth stage the frequency and abundance of this species group abruptly decrease. The herbs *V. myrtillus*, *V. vitis-idaea* are abundantly spreading from the third to the fourth stages: *Carex globularis* and *Rubus chamaemorus* appear only at the beginning and spread at the end of the fourth stage.

4. Discussion

4.1. Species composition and diversity of epixylic vegetation

The share of vascular plants found on decaying wood is lower than in comparison with the experimental data of Jonsson and Esseen (1998), which characterizes plant composition in small-scale disturbed patches. We observed an 18% share of vascular plants on the fallen spruce logs, whereas the above authors report 41% on disturbed patches. The small number of vascular plants in our case could be explained by the fact that we considered the well recognized in the field CWD; the mounds of microrelief of CWD origin could be colonized by a greater variety of plant species. The lichens are presented by 21 species on the fallen logs (17% of the total species list), however they are absent both on the mineral disturbed soil and on the humus disturbed patches (Jonsson and Esseen, 1998). The ratio between mosses and hepatics on decaying wood in our study fully agrees with the data collected by Andersson and Hytteborn (1991) on decaying wood in Sweden. In our study, mosses and hepatics constitute 44% and 21% of the species list, respectively. The mosses on the small patches of disturbed soil are represented by a lower number of species (32–34%, Jonsson and Esseen, 1998). It could be explained by the absence of

epiphytes and the generally fewer number of species specialized on such patches. However, the number of hepatics species on those patches is higher.

The average species number of the moss–lichen layer per plot varies slightly in comparison with variation of the total species number by stages.

The epixylic vegetation in different conditions is often compared without specification of the stage of evergrowing (McAlister, 1997). Differences in the availability of CWD of different age, the speed of overgrowing in different conditions, as well as dependence of species' abundance on the time of their appearance and disappearance tend to create uncertainties in the interpretation of results. Studying the stages of microsuccession of vegetation on logs during stages of wood decay provides information only on the link between abundance of the species (groups) and wood decay stages and indirectly indicates dynamics of epixylic vegetation (Södeström, 1988b, 1989; Andersson and Hytteborn, 1991; Muhle and LeBlanc, 1975; McCullough, 1948; Shorohova and Shorohov, 1999). The vegetation succession and wood decomposition are not synchronic processes, they are driven by different factors.

The composition and structure of epixylic vegetation depends on, in addition to the wood decay class, the species of the log (Södeström, 1988b, 1989; Andersson and Hytteborn, 1991; McAlister, 1997), ecological conditions of the forest community (namely moisture, lightness, coverage of the herb layer), etc. (Muhle and LeBlanc, 1975; Istomina, 1993), successional stage of the forest, its management status and availability of decaying wood for inhabiting (Andersson and Hytteborn, 1991; Gustaffson and Hallingbäck, 1988; Södeström, 1988a; Herben and Södeström, 1992; Rambo and Muir, 1998), stem diameter, bark cover and wood texture (Södeström, 1988a,b, 1989; Andersson and Hytteborn, 1991). For a more precise reconstruction of succession, as well as for a more accurate determination of the impact of ecological factors on the parameters of epixylic communities, the processes of wood overgrowing and decomposition should be considered separately. The stages of overgrowing should be distinguished by the features of the vegetation itself.

The diversity of epixylic microgroups during the first stage can be explained by the fact that the overgrowing of a substrate takes place in many ways accidentally and under the influence of external factors. If the vegetation cover is sparse, competition is almost absent. The diaspores of most species can germinate there. The chief restriction for the possibility of the species' germination is its ability to grow on such substrate. There are relatively few species that can grow on a naked substrate. The first stage is the poorest in terms of the species number; more than half of the species have single occurrences. The maximum value of the Pielou index (Table 4) reflects this pattern—small patches of different species forming open mosaics without any pronounced dominants.

The number of species found during the middle stages of overgrowing is significantly higher than during the first and last ones. The increase of the species number during the second stage may be due, on the one hand, to a longer time period and

exposure; on the other hand, it may indicate more favorable conditions for greater numbers of species. In view of the fact that the physical parameters of the substrate (decaying wood) are better compared to those of the surrounding soil, the increase in both the number and cover of the ground flora species on this stage is especially demonstrative. The plots of the third stage, characterized by the dominance of the ground flora species, are very different physionomically from those of the previous stages. However, the species composition changes insignificantly. The decrease of the species number occurs mainly at the expense of the least abundant earliest species. Many species typical for the second stage can still be found in the microgroups, but their abundance decreases dramatically. The change of the dominants takes place: *P. pulcherrimum* is replaced by *P. schreberi*.

The fourth stage is distinguished by the spread of vascular plants; the number of the lichens and bryophytes decreases, whereas the number of vascular plants increases. The number of species of the moss–lichen layer per individual stages and per plot of the last stage coincides with the earliest stages. However, the difference between the Shannon and Pielou indexes indicates the principal differences in structure of the microgroups (Table 4). Low numbers of species and high characteristics of biodiversity and evenness during the first stage correspond to the process of germinating in the new habitat. The low species number and low biodiversity indexes during the fourth stage suggest well-developed community structure. The moss cover on the decaying wood becomes similar to that on the ground. Species with other substrate preferences or generalists that are weak competitors in these conditions have disappeared. Epixylic vegetation in the *Sphagnum–Myrtillus* type of spruce forest (V4) turned out to be the only exception to this rule. The Shannon index there has reliably higher values (1.25) than in the other sites (0.76–1.01). It can be explained that such mesophytic as hygrophytic large mosses grow without excluding each other; many liverworts are abundant there because of high moisture content.

4.2. Types of microsuccession

The described sequences of vegetation can be considered as three types of microsuccession. The types of microsuccession were distinguished based on the results of the Kraskal–Wallis and Duncan's tests. The tests showed the homogeneity of all material except for the site L2. The microsuccession on the site V4 significantly differs from those on the all other sites by presence of one more stage.

The *first type*, central to this paper, is typical for spruce forests with well-developed feather moss cover (the projective cover exceeds 60%); dominance of *V. myrtillus and V. vitis-idaea* is presented on the sites K, L1, L3, V1, V2, V3. It is characterized by the dominance of the epiphytic species (mostly *P. pulcherrimum*) during the first–second stages. The epigeous species germinate during the first stage and dominate during the third–fourth stages. The abundance of generalists and epixylics is insignificant and varies on different sites.

The *second type* is identified by the low abundance of epigeous species and significant share and dominance of generalists during the latter stages of overgrowing. This succession type is connected with the herb-rich forests where the rich litter fall of deciduous species suppresses the moss cover (represented by small patches mainly at the base of living trees or on the well decomposed woody debris (L2)). These ground patches are formed by the generalists as well. Generally, the process of overgrowing of the decaying logs can be interpreted as a gradual increase in similarity of epixylic vegetation to the ground vegetation. In this community, in contrast, there is an extinction of the ground flora species as these are not capable of existing in given conditions. In the herb-rich forests, the decaying wood represents the refuge where the ground flora species continue to grow. The succession state of the stand is assumed to be replacement of aspen with spruce. When aspen disappears from the tree canopy, the amount of litter fall will decrease; the ground flora mosses begin to actively germinate on the soil. Probably, decaying wood will be one of the sources of their spread.

The *third type* is marked out by the presence of the stage where one group of ground flora mosses is replaced by another. In the *Sphagnum–Myrtillus* spruce forest (V4), the large feather mosses are almost absent in the ground cover. They successfully exist on the micro-relief mounds represented by bases of living trees, fallen decaying logs, etc. As in the previous case, the decaying wood plays the role of refugee host for the species that are not typical to the ground cover. In this biotope, the large feather mosses have weaker competitive ability in comparison with *Sphagnum* mosses, but they quickly germinate on the woody substrate and grow there until they are replaced with the ground cover dominants.

The three types of succession of epixylic vegetation result from the ground cover of studied forest types. If the biotope conditions are favorable for the large feather mosses, the process of overgrowing amounts to the spread of large feather mosses; during this time other species groups have an opportunity to germinate, grow and cede the place to the ground flora species. If the biotope conditions are unfavorable for the large feather mosses, they fall within a role of "temporal lodgers", dominating on the middle stages of overgrowing.

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