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Epiphytic bryophytes in old growth forests of slopes, screes and ravines in north-west Latvia

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Abstract

Little is known about the ecology of epiphytic bryophytes in broad-leaved forests of slopes, screes and ravines. Factors determining the epiphytic bryophyte distribution in such forests were investigated. In total 45 epiphytic bryophyte species were found (12 of them were signal species, including three specially protected species in Latvia – *Antitrichia curtipendula*, *Neckera crispa* and *Plagiothecium latebricola*). The total number of bryophyte and number of signal species were higher on tree species with relatively basic bark pH (*Acer platanoides*, *Ulmus glabra*, *Fraxinus excelsior*, *Populus tremula*, *Sorbus aucuparia*, *Tilia cordata*, *Salix* sp.), but lower on tree species with acidic bark (*Alnus glutinosa*, *Betula pendula*, *Picea abies*). Tree diameter, age and distance from tree to top of slope were not related to epiphytic bryophyte distribution. The highest bryophyte species richness (including signal species) was found up to a 0.5-m height on the southern exposure of trees and on the upper side of inclined trees (on south exposure of trees on north facing slopes, and on east exposure of trees – on west facing slopes).

Key words: broad-leaved forests, bryophyte, distribution, epiphyte.

Introduction

The broad-leaved forests in Latvia are highly fragmented by agricultural land-use on previous woodland cleared for tillage (Dumpe 1999). European broad-leaved forests in Latvia are mostly restricted in river valleys or slopes, lake islands and plains in their ancient distribution areas (Priedītis 1999). Many Central European plant and animal species are associated specifically with these forests (Priedītis 2000). Rich epiphytic bryophyte diversity (including many rare and threatened species) is found in natural broad-leaved forests (Priedītis 2000; Bambe, Lārmanis 2001; Ek et al. 2001).

The understorey vegetation (Priedītis 1999), bryophyte flora (Āboliņa 1968; Āboliņa 2001a; Āboliņa 2001b; Bambe, Lārmanis 2001; Bambe 2002; Āboliņa, Rēriha 2004) and lichen flora (Piterāns 2001) have been studied in broad-leaved forests of Latvia, but knowledge about epiphyte ecology is lacking (Znotiņa 2003).

Zilie kalni of Slitere National Park is a ravine system with little previous human impact. Due to its geological history and climate, Zilie kalni (Sarma 1958) supports some of the most important undisturbed Latvian forests of slopes, screes and ravines with high biodiversity, including many rare and threatened plant species (Seile, Rēriha 1983; WWF Project 1992).

Survey of natural old growth broad-leaved forests as woodland key habitat (WKH) in Latvia began in 1997. Rare and protected bryophyte, lichen, insect and fungi species are used as indicators for identification of these forests (sensu Ek et. al 2001), but little is known about the ecology of these species in Latvia.

The most important factors affecting the distribution of epiphytic bryophyte species are forest stand age, tree age and diameter (Barkman 1958; Kuusinen 1996; Hazell et al. 1998; Kuusinen, Penttinen 1999; Aude, Poulsen 2000; Hedenås, Ericson 2000; Ojala et al. 2000), as well as tree species (Āboliņa 1968; Snäll et al. 2004), tree bark physical and chemical properties (Apinis, Diogucs 1935; Apinis, Lācis 1936; Smith 1982; Smith 1996; Weibull 2001) and microclimate (John, Dale 1995; Hazell et. al 1998; Hazell, Gustaffson 1999; Thomas et al. 2001; Bambe 2002).

The cover of epiphytic bryophytes is much higher on deciduous tree species, such as *Fraxinus excelsior*, *Acer platanoides*, *Ulmus glabra*, *Tilia cordata* (Snäll et al. 2004), *Alnus incana* and *Populus tremula* as compared to conifers (Āboliņa 1968).

Dense bark of old trees with cracks where dust and humus has accumulated is more suitable for epiphyte growth (Znotiņa 2003) but smooth, bare bark, with low air humidity is less suitable (John, Dale 1995). The bark of older trees is porous, maintaining a humidity more favourable for better bryophyte growth (Āboliņa 1968).

Tree bark is rougher on the basal part of tree stems, explaining why bryophytes favour tree bases in comparison with the smooth upper part of tree stems, with low humidity and less nutrients (John, Dale 1995; Znotiņa 2003).

Air humidity is one of the most important factors effecting the distribution and development of bryophytes (Bambe 2002). Dense epiphytic bryophyte cover is observed in deep valleys of rivers as well as at brook edges where the air humidity is high (Āboliņa 1968).

Tree bark pH is an important factor determining epiphyte distribution (Weibull 2001, Znotiņa 2003). Bryophyte species each have an optimum substrate pH range (Apinis, Diogucs 1935; Apinis, Lācis 1936). Bark pH differs among tree species (Āboliņa 1968) and coniferous trees have a lower pH than deciduous trees (Barkman 1958; Smith 1982).

The relation between height and exposure on tree stems and epiphyte community composition have been described only in a few reports (John, Dale 1995; Moe, Botnen 1997; Hazell, Gustafsson 1999; Thomas et al. 2001).

The composition of epiphytic species on tree stems varies in relation to relative humidity, light intensity and bark properties (Smith 1982). Epiphyte cover is increased on north and south exposures on basal parts of tree stems (John, Dale 1995), but all of the above factors together determine the spatial distribution of epiphytic bryophytes on trees (Thomas et al. 2001). The aim of this work was to describe the epiphytic bryophyte flora and determine the factors affecting WKH indicator species and special protected species distributions in Zilie kalni of Slitere National Park of north-west Latvia.

Materials and methods

Study area

The Study area (Fig. 1) is situated in the north-west part of Latvia, Slītere National Park (22° 10' 50.1"E, 59° 35' 29.0" N). The mean annual air temperature is 5.9 °C (Sarma 1958) and the mean annual precipitation is 573 mm (Seile, Rēriha 1983).

Zilie kalni is a bow-shaped north-facing slope, relative height up to 42.5 m, spanned

Fig. 1. Map of the Baltic states showing the study area (•).

by side ravines more than 20 km along (from west to south-east direction). Old growth mixed broad-leaved forest stands are the dominant forest type (WWF Project 1992).

Data sampling

The field work was conducted in July 2003 and March 2004 in Zilie kalni (Fig. 1). One north-facing slope and one west-facing side ravine were studied.

On the north-facing slope three 2-m-wide parallel transects (about 67 m long) leading downhill (from south to north direction) were randomly established. All trees with diameter at breast height ≥ 0.10 m and canopies crossing the transect were sampled. Height and distance to the top of slope were determined for each tree. The west-facing slope was selected on a side ravine, where nine broad-leaved trees (diameter at breast height ≥ 10 cm) were selected.

Tree cores were removed by an increment corer and tree rings were counted on a Lintab table equipied with a Leica microscope (MS 5) for determination of tree age.

Cover of bryophyte species was determined using the 5-point Braun-Blanquet scale (Kent, Cooker 1992) on different sides (N, S, E, W) and heights (lowest part – until 0.5 m, highest part – 0.5 ÷ 1.5 m) of tree stems (eight plots on each tree) on all trees.

Bryophyte species that could not be identified in the field were collected for identification in the laboratory. Species nomenclature follows (Hallingbäck, Holmåsen 2000; Smith 1996a; Smith 1996b).

Determination of tree bark pH

Tree bark pH was determined in laboratory after Kermit and Gauslaa (2001). Bryophytes and lichens were removed from tree bark and samples of tree bark were cut. Each sample weighed approximately 0.5 g. There was difficulty in removing bark from some trees, therefore 24 of 76 samples weighed less than 0.5 g. Each bark sample was shaken in a 20-ml 1 M KCl solution for 1 h and pH was determined with a pH-meter (GPH 014, *Greisinger Electronic*).

Table 1. Epiphytic bryophyte species occurrence on tree species and pH amplitude (in both of slopes). *, signal species

Bryophyte species	Tree species (number of trees)												pH		
	Acer platanoides (7)	*Ulmus glabra* (7)	*Fraxinus excelsior* (13)	*Populus tremula* (15)	*Salix sp.* (2)	*Sorbus aucuparia* (2)	*Tilia cordata* (1)	*Alnus glutinosa* (2)	*Betula pendula* (11)	*Picea abies* (16)	Number of trees	Number of tree species	pH min	pH max	pH average
Amblystegium serpens	2	3	4	8	1	-	-	1	1	1	21	8	4.6	6.2	5.0
*Anomodon longifolius**	-	-	2	-	-	-	-	-	-	-	2	1	5.9	6.2	6.0
*Anomodon viticulosus**	-	1	-	-	-	-	-	-	-	-	1	1	6.2	6.2	6.2
*Antitrichia curtipendula**	1	-	1	-	-	-	-	-	-	-	2	2	5.4	5.6	5.5
Brachythecium oedipodium	-	-	2	1	-	-	-	-	-	-	3	2	5.3	5.9	5.5
Brachythecium rutabulum	2	2	4	6	2	1	-	1	1	2	21	9	3.6	6.2	4.4
Brachythecium populeum	1	-	-	1	1	-	-	-	-	-	3	3	5.3	5.4	5.3
Brachythecium velutinum	1	-	-	1	-	-	-	-	-	1	3	3	3.9	5.6	4.4
Dicranum montanum	-	1	-	3	-	-	-	2	10	9	25	5	3.4	5.8	3.9
Dicranum scoparium	-	-	-	3	-	-	-	2	11	3	19	4	3.4	5.4	3.9
Eurhynchium angustirete	-	-	-	1	-	1	-	-	-	-	2	2	5.3	5.8	5.6
Eurhynchium hians	2	1	-	4	-	-	-	-	-	5	12	4	3.8	6.8	4.5
Eurhynchium striatum	3	-	6	9	-	1	-	2	6	6	33	7	3.4	6.8	4.2
Eurhynchium pulchellum	-	-	-	-	-	-	-	-	1	1	2	2	3.6	3.8	3.7
Frullania dilatata	4	3	11	12	1	2	-	-	1	-	34	7	4.5	6.8	5.3
Homalothecium sericeum	3	4	5	9	1	-	-	-	2	-	24	6	3.8	6.8	4.7
*Homalia trichomanoides**	2	4	8	6	1	-	-	-	-	-	21	5	4.9	6.2	5.4
Hypnum cupressiforme	3	3	4	12	2	2	1	2	8	13	50	10	3.1	6.8	4.1
*Isothecium alopecuroides**	2	2	2	1	1	-	1	-	-	1	10	7	3.8	6.2	4.8
*Isothecium myosuroides**	1	3	6	1	1	-	-	-	-	1	13	6	4.2	5.6	4.8
Lepidozia reptans	-	-	1	-	-	-	-	-	4	-	5	2	3.6	5.3	4.0
Leucodon sciuroides	1	3	5	3	-	-	-	-	-	-	12	4	5.2	6.2	5.7
Lophocolea heterophylla	2	2	3	3	2	1	-	2	7	4	26	9	3.4	5.9	4.0
*Metzgeria furcata**	3	5	7	12	2	2	1	1	3	-	36	9	3.6	6.8	4.7
Mnium stellare	2	3	3	7	1	-	-	1	1	-	18	7	4.9	5.9	5.2
*Neckera complanata**	5	3	7	10	2	2	-	-	-	-	29	6	4.9	6.8	5.3
*Neckera crispa**	2	-	1	1	-	-	-	-	-	-	4	3	5.3	6.8	5.7
*Neckera pennata**	-	1	2	-	-	-	-	-	-	-	3	2	5.9	6.2	5.9
Plagiomnium affine	-	-	-	1	-	-	-	-	-	-	1	1	5.4	5.4	5.4
Plagiomnium undulatum	-	2	1	-	-	-	-	-	-	1	4	3	3.9	5.9	4.3
Plagiochila porelloides	1	2	1	4	-	-	-	-	2	1	11	6	5.8	6.2	5.9

(continued)

Bryophyte species	Tree species (number of trees)												pH		
	Acer platanoides (7)	*Ulmus glabra* (7)	*Fraxinus excelsior* (13)	*Populus tremula* (15)	*Salix sp.* (2)	*Sorbus aucuparia* (2)	*Tilia cordata* (1)	*Alnus glutinosa* (2)	*Betula pendula* (11)	*Picea abies* (16)	Number of trees	Number of tree species	pH min	pH max	pH average
Plagiothecium cavifolium	-	-	-	1	-	-	-	-	-	-	1	1	5.4	5.4	5.4
Plagiothecium curvifolium	1	-	1	7	1	1	-	-	6	3	20	7	3.6	6.8	4.4
Plagiothecium denticulatum	-	-	1	-	1	1	-	1	6	5	15	6	3.4	5.9	3.8
Plagiothecium laetum	1	-	1	1	1	-	-	-	1	3	8	6	3.8	6.2	4.2
*Plagiothecium latebricola**	-	-	-	-	-	-	-	1	-	-	1	1	4.3	4.3	4.3
Platygyrium repens	-	2	2	-	-	-	1	-	1	2	8	5	3.8	5.9	4.1
Ptilidium pulcherrimum	1	-	-	-	-	-	-	1	7	-	9	3	3.6	5.8	4.0
Pylaisia polyantha	-	2	2	3	1	1	-	1	4	2	16	8	4.6	6.2	4.8
Pleurozium schreberi	-	-	-	-	-	-	-	-	1	-	1	1	4.5	4.5	4.5
Radula complanata	7	5	12	14	2	2	1	1	3	1	48	10	3.8	6.8	4.8
Sanionia uncinata	-	-	-	1	-	-	-	-	1	-	2	2	3.6	6.8	5.2
Thuidium delicatulum	-	-	-	-	-	-	-	-	1	-	1	1	3.8	3.8	3.8
Thuidium tamariscinum	-	1	3	5	-	-	-	2	3	-	14	5	3.6	5.9	4.3
*Ulota crispa**	3	2	8	12	1	1	1	1	1	2	32	10	4.0	6.8	5.0
min	5.4	5.5	5.2	4.8	4.7	5.3	5.1	3.6	3.6	3.1					
max	6.1	6.2	6.0	6.8	5.1	5.3	5.1	4.6	4.8	4.2					
average	5.7	5.7	5.5	5.2	4.8	5.3	5.1	3.9	3.9	3.6					

Data processing

Bryophyte community structure and gradients were analysed with the TWINSPAN and DECORANA programme package (PC-ORD for Windows, B. McCune and M. J. Mefford 1999. Multivariate analyses of Ecological Data Version 4.17, Oregon, USA), DCA (Detrended correspondence analysis). Relations of bryophyte species with environmental variables were determined by regression analysis (MS Excel) and Kendall's correlation (SPSS for Windows, Release 11.5.0, *SPSS inc.*). Bark pH values were converted to H^+ concentration before calculation of mean pH values.

Results

Forest stand

The studied forests were broad-leaved mixed tree forest stand with dominant *Picea abies*, *Populus tremula* and *Fraxinus excelsior*. The cover of bryophytes were estimated on 76 trees of 10 species. Uneven age structure was observed for trees, where the oldest was *Ulmus glabra* – 250 years. Dead wood was observed in various decay stages and cut tree stumps were not found, indicating minimal human impact.

Bryophyte occurrence

In total, 45 epiphytic bryophyte species were recorded – 38 Bryopsida and seven Hepaticopsida. Eight indicator species of old growth forests (Ek et al. 2001) – *Neckera complanata*, *Isothecium myosuroides* (Latvian Republic Cabinet of Ministers 2001), *Metzgeria furcata*, *Neckera pennata*, *Ulota crispa*, *Isothecium alopecuroides*, *Anomodon longifolius*, *Anomodon viticulosus*, *Homalia trichomanoides*) and three WKH specialist species specially protected in Latvia (*Antitrichia curtipendula*, *Neckera crispa* and *Plagiothecium latebricola*), were found. Further the term "signal species" will include both the WKH indicator species and the specially protected species.

The most common bryophyte species were *Hypnum cupressiforme* and *Radula complanata* (Table 1). Among the signal species, *Ulota crispa*, *Metzgeria furcata* and *Isothecium alopecuroides* had the widest ecological valence on trees.

Preference of bryophyte species for tree species

The number of epiphytic bryophyte species varied depending on substrate tree species. The richest bryophyte flora was found on *Populus tremula* and *Fraxinus excelsior* (Fig. 2). The number of signal species was highest on *Fraxinus excelsior*. The lowest number of bryophyte species was on *Picea abies*.

Dicranum montanum and *Dicranum scoparium* were found on *Betula pendula*. *Radula complanata* was exclusive to *Populus tremula*, *Fraxinus excelsior* and *Acer platanoides*.

Relation of the tree DBH, height, age, pH and tree distance to top of slope and the distribution of bryophytes

Kendall's correlation coefficients between the number of bryophyte species, number of signal species, tree bark pH, DBH, height, age and tree distance to top of slope were determined (Table 2; Fig. 3). The number of bryophyte species was significantly related to

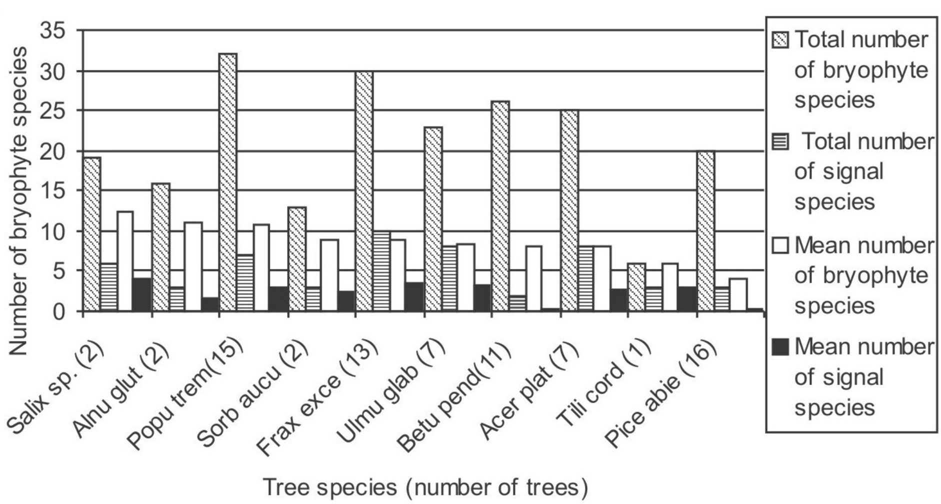

Fig. 2. Total number of bryophyte species on tree species and mean mumber per tree (in both of slopes).

Table 2. Nonparametric correlations (Kendall's correlation coefficients) among variables (on both slopes). **, correlation is significant at the 0.01 level (2-tailed); *, correlation is significant at the 0.05 level (2-tailed); DBH, tree diameter at breast height

	Number of signal species	DBH	Tree bark pH	Tree age	Tree height	Distance to top of slope
Number of species	0.536**	0.142	0.208*	0.035	0.325**	-0.016
	Number of signal species	0.013	0.469**	0.066	0.209	0.024
		DBH	-0.172	0.135	0.654**	-0.001
			Tree bark pH	0.052	-0.053	-0.009
				Tree age	0.124	0.077
					Tree height	0.052

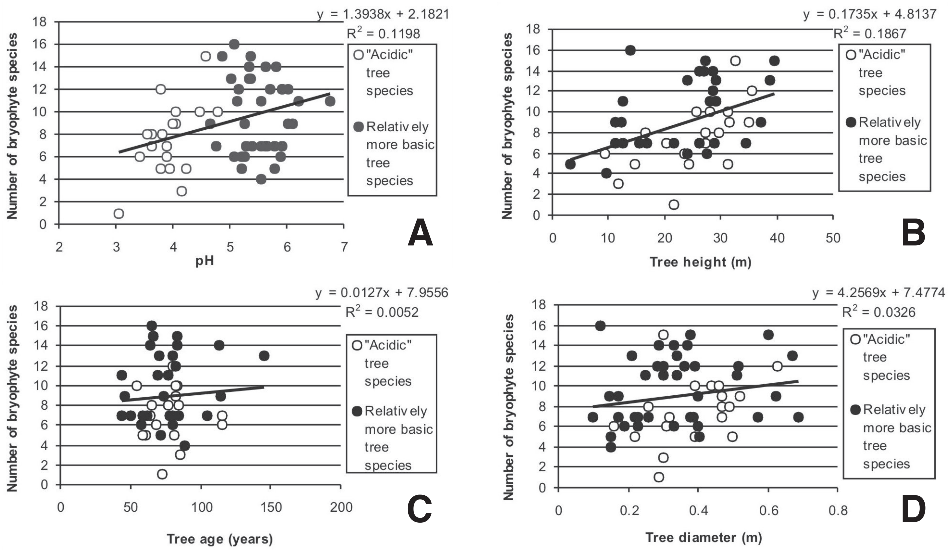

Fig. 3. Relationship between the total number of bryophyte species and tree bark pH (A), tree height (B), tree age (C), tree diameter at breast height (D).

tree height and bark pH. Number of signal species was correlated significantly only with tree bark pH (Table 2).

Tree bark pH

Tree bark pH varied between 3.1 and 6.8 for the studied trees, being lowest for *Picea abies* and *Betula pendula* and highest for *Populus tremula* and *Ulmus glabra* (Table 1). Both the number of bryophyte species and the number of bryophyte signal species was higher on trees with higher bark pH (Fig. 2; Table 1).

Based on the bryophyte preference on tree species, it was possible to divide trees into

Table 3. Number of bryophyte plots with bryophytes in various heights and exposures on trees (in both of slopes). N, north; S, south; E, east; W, west; *, signal species

Bryophyte species	Exposure				Height (m)	
	N	S	E	W	0 - 0.5	0.5 - 1.5
Amblystegium serpens	10	15	14	14	21	32
*Anomodon longifolius**	-	-	-	1	-	1
*Anomodon viticulosus**	1	2	2	2	4	3
Brachythecium oedipodium	-	1	-	-	1	-
Brachythecium populeum	-	-	2	-	1	1
Brachythecium rutabulum	3	7	3	1	14	-
Dicranum montanum	19	32	25	21	56	41
Dicranum scoparium	11	17	6	6	28	12
Eurhynchium angustirete	1	1	2	2	6	-
Eurhynchium hians	4	1	2	2	8	1
Eurhynchium striatum	16	21	22	20	64	15
Frullania dilatata	31	28	29	27	34	81
Homalothecium sericeum	18	13	11	13	17	38
*Homalia trichomanoides**	14	13	9	6	31	11
Hypnum cupressiforme	46	55	47	49	139	58
*Isothecium alopecuroides**	7	6	7	5	20	5
*Isothecium myosuroides**	10	12	9	9	25	15
Lepidozia reptans	1	5	2	5	7	6
Leucodon sciuroides	5	2	7	8	12	10
Lophocolea heterophylla	11	17	9	16	29	24
*Metzgeria furcata**	23	28	34	27	65	47
Mnium stellare	11	5	7	10	26	7
*Neckera complanata**	33	29	29	31	55	67
*Neckera crispa**	7	7	7	4	13	12
*Neckera pennata**	1	2	3	1	5	2
Plagiochila porelloides	2	2	-	2	5	1
Plagiomnium undulatum	-	1	1	1	3	-
Plagiothecium cavifolium	1	1	1	1	4	-
Plagiothecium curvifolium	9	13	14	11	40	7
Plagiothecium denticulatum	4	9	4	5	16	6
Plagiothecium laetum	1	1	2	3	7	-
*Plagiothecium latebricola**	1	1	1	-	3	-
Platygyrium repens	2	1	1	1	4	1
Ptilidium pulcherrimum	6	4	2	7	8	11
Pylaisia polyantha	2	8	5	6	13	8
Radula complanata	52	51	50	46	69	130
Thuidium delicatulum	-	-	1	1	2	-
Thuidium tamariscinum	11	11	8	12	30	12
*Ulota crispa**	12	19	15	17	9	54
Total number	386	441	393	393	894	719

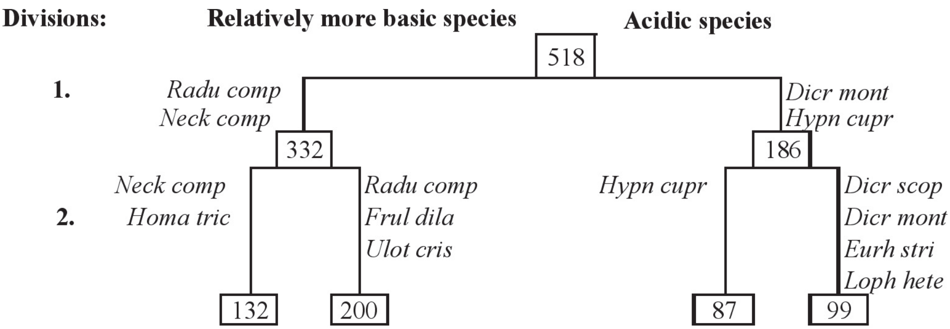

Fig. 4. TWINSPAN dichotomous division of epiphyte plots on both slopes. Indicator species are shown. *Radu comp*, *Radula complanata*; *Neck comp*, *Neckera complanata*; *Homatric*, *Homalia trichomanoides*; *Frul dila*, *Frullania dilatata*; *Dicr mont*, *Dicranum montanum*; *Hypn cupr*, *Hypnum cupressiforme*; *Dicr scop*, *Dicranum scoparium*; *Eurh stri*, *Eurhynchium striatum*; *Loph hete*, *Lophocolea heterophylla*.

those with relatively more basic bark (*Acer platanoides*, *Ulmus glabra*, *Fraxinus excelsior*, *Populus tremula*, *Sorbus aucuparia*, *Tilia cordata*, *Salix* sp. and with acidic bark (*Alnus glutinosa*, *Betula pendula* and *Picea abies*).

The first TWINSPAN division level separated plots on the basis of acidic- and relatively more basic-preferring bryophyte species (Fig. 4). Signal species, like *Neckera crispa*, *Neckera complanata* and also common species *Leucodon sciuroides* were found mostly on relatively more basic trees (Table 1). *Dicranum scoparium*, *Dicranum montanum* and *Lepidozia reptans* were generally distributed on acidic trees. *Hypnum cupressiforme* and *Brachythecium rutabulum*, *Plagiothecium curvifolium* and *Radula complanata* did not show any relation with tree species and bark pH.

Bryophyte vertical and horizontal spatial distribution on trees

The occurence and cover of bryophyte species was studied on various heights (below 0.5 m and between 0.5 and 1.5 m) and exposures (N, W, S, E) on the tree stem, together eight plots on each tree. More bryophyte species with high cover were found on the tree base (Table 3), e.a., *Brachythecium rutabulum*, *Eurhynchium angustirete* and *Plagiomnium undulatum*. The occurrence of *Radula complanata*, *Frullania dilatata*, *Homalothecium sericeum* was higher between 0.5 and 1.5 m on the tree stem.

The second TWINSPAN division level separated epiphytic communities in the different parts of the tree stem. The TWINSPAN indicator species Homalia trichomanoides and *Neckera complanata* were distributed more on the tree base, but *Radula complanata*, *Frullania dilatata* and *Ulota crispa* were found more at a 0.5 to 1.5 m height. *Hypnum cupressiforme* did not show any relation with height. *Dicranum scoparium*, *Dicranum montanum*, *Eurhynchium striatum* and *Lophocolea heterophylla* grew up to a height of 0.5 m only on acidic trees.

Differences were observed between bryophyte species occurrence on trees of the north slope of the Zilie kalni escarpment and east slope of the side ravine. Bryophyte occurrence was higher on the south exposure of trees on a north-facing slope (385 of all 1414 plots), but on the east exposure of trees on a west-facing slope (56 of all 198 plots).

The highest number of plots lacking bryophytes was observed on the north exposure on trees in the studied area (on both slopes). Plots with bryophytes (including signal species) were more common on the south exposure on trees (Table 3). The number of plots without bryophytes was similar on east and west exposures.

The species gradients extracted by DCA did not show any relation with height and direction of exposure on tree stems.

Discussion

The significance of tree bark pH

Among the studied factors, tree bark pH showed the best relationship with distribution of bryophyte species, which is consistent with other studies (Āboliņa 1968; Weibull 2001; Löbel et al. 2006).

In general, bark pH is a specific attribute for each tree species. Deciduous trees (except *Betula pendula* and *Alnus glutinosa*) have relatively higher bark pH in comparison with coniferous trees. At the same time, a specific pH amplitude exists for bryophyte species depending on substrate (Apinis, Diogucs 1935; Apinis, Lācis 1936; Barkman 1958). However, environmental factors (soil dust, acid rain) can change the value of tree bark pH, and the distribution of epiphyte species can change respectively (Barkman 1958).

TWINSPAN analysis clearly divided plots by tree species – relatively more basic (bark pH above 4.4) and acidic (below 4.4). The highest number of bryophyte species and especially the signal species, e.a., *Anomodon* sp. and *Neckera crispa* were found on reltively more basic tree species. On acidic trees, there was a lower number of species, fewer signal species (*Metzgeria furcata*, *Ulota crispa*, *Isothecium* sp.) and species with wide ecological valence (like *Hypnum cupressiforme* and *Brachythecium rutabulum*). The low epiphyte diversity on acidic trees can be explained by a possible toxic effect of tannins and resins in the bark of *Betula pendula* and coniferous trees (Barkman 1958; Gauslaa 1995).

Several authors (Hazell et al. 1998; Ojala et al. 2000) have described *Populus tremula* as a tree species which is particularly rich in epiphytes. However, in the present study, *Fraxinus excelsior* hosted a similar number of bryophyte species as *Populus tremula*.

Relationships between bark pH and tree age (Barkman 1958) and bark pH and tree diameter (McGee et al. 2002) have previously been reported, which was also found in our study (both for single tree species and for stand), but our sample size for trees was rather low.

Influence of tree age and diameter

Several authors have described an increased epiphyte richness on older trees with larger stem diameter (Trynoski, Glime 1982; Hazell et al. 1998; Aude, Poulsen 2000; Snäll et al. 2004). Some species prefer very old trees (Kuusinen, Siitonen 1998), which can be explained by relatively slow growth and colonisation rates (Crites, Dale 1998) and with changes of bark structure. With ageing of the tree, the bark structure becomes more suitable (thick and rough) for epiphyte growth (Hyvärinen et al. 1992). Also, there is more surface area for colonisation on larger trees (Lyons et al. 2000).

In our study, no significant correlation between the diversity of epiphytes and the tree age and diameter (both in general and for single tree species) was found. Possible explanations may be:

(i) in previous studies, the forest microclimate and the development history differed from the studied broad-leaved forest;

(ii) in a forest with long continuity (like the studied stand), microhabitat availability and not dispersal is the limiting factor for the establishment of epiphyte species.

A slight positive relationship was found only between tree height and the number of bryophyte species. This relation was observed for the forest stand in total, but not within tree species. The relatively lower species richness on smaller (lower) trees can be explained by shading from other trees (Lyons et al. 2000).

Influence of microclimate

Aspect of epiphytes on the tree stem is a valuable tool for detailed study of the microclimate and microhabitat niche of bryophyte species. TWINSPAN analysis divided plots into four groups based on bryophyte species: (i) growing at the base (below 0.5 m) of relatively basic trees; (ii) growing higher (0.5 to 1.5 m) on stems of relatively basic trees; (iii) growing at the base (below 0.5 m) of acidic trees; (iv) growing on acidic trees without any height preference (Fig. 4.).

The highest number of species was found at the basal part of tree stems (0.5 m). There were no species preferring the higher part of tree stems on acidic trees. *Hypnum cupressiforme*, a widely distributed species without preference to a specific substrate (Āboliņa 1968; Weibull 2001), was distributed throughout the tree stem. The low species diversity on the upper part of acidic tree stems can be explained by desiccation of bark, which is more pronounced for coniferous in comparison with deciduous trees, and with bark scaling of conifers (Barkman 1958). The base of all trees was covered with species from the surrounding soil, like *Plagiomnium affine*, *Eurhynchium striatum*, *Plagiomnium undulatum*. However, the base of basic trees provided habitat also for signal species like *Neckera complanata*, *Homalia trichmonoides*, *Antitrichia curtipendula*, *Neckera crispa*, *Anomodon viticulosus* and *Anomodon longifolius*. The epiphyte diversity decreased higher on the tree stem (between 0.50 and 1.50 m). On basic trees higher parts were typically inhabited by pioneer species *Radula complanata*, *Frullania dilatata*, *Ulota crispa*, (Barkman 1958; Trynoski, Glime 1982) adapted to desiccation (Moe, Botnen 1997).

At the tree base, high bryophyte diversity is favoured due to higher relative humidity (Barkman 1958; Āboliņa 1968; John, Dale 1995; Bambe 2002) and the physical and chemical nature of tree bark (Smith 1982). Thick and rough bark provides sheltered microhabitats for the establishment and growth of bryophytes (Barkman 1958). Also, uncovered roots of trees provide various microhabitats for bryophytes (personal observation). The high bryophyte diversity at the tree base (below 0.50 m) indicates that the humidity and the physical properties of bark (thickness, cracks) are limiting factors for the local distribution of the epiphyte species.

Several authors have described a higher bryophyte cover on the north exposure of trees and less on the south, east and west. Relatively low light and temperature and relatively high humidity on the north-facing slope which provide suitable conditions for bryophyte growth (Barkman 1958; Trynoski, Glime 1982).

In our studied forest stand, a higher number of bryophyte species, including signal species, was found on the southern exposure, but lower, on the northern part of trees. This can be explained by the relief of the studied site – on the northern slope trees were leaning northwards. On the upper part of leaning trees, there is a suitable microclimate for bryophyte growth, because the humidity here is maintained for a relatively longer period (Barkman 1958). The influence of the inclination on the epiphytic vegetation is due to precipitation and general moisture conditions (Moe, Botnen 1997).

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Epifītiskās sūnas dabiskos nogāžu un gravu mežos ziemeļrietumu Latvijā

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Kopsavilkums

Epifītisko sūnu ekoloģija nogāžu un gravu mežos ir maz pētīta. Dotajā pētījumā noskaidroti faktori, kas ietekmē epifītisko sūnu izplatību šajos mežos. Kopumā konstatētas 45 epifītisko sūnu sugas, no kurām 12 bija signālsugas, tai skaitā, arī trīs īpaši aizsargājamas sūnu sugas Latvijā – *Antitrichia curtipendula*, *Neckera crispa* un *Plagiothecium latebricola*. Kopējais sūnu sugu un signālsugu skaits bija augstāks uz kokiem ar relatīvi bāzisku mizas pH (*Acer platanoides*, *Ulmus glabra*, *Fraxinus excelsior*, *Populus tremula*, *Sorbus aucuparia*, *Tilia cordata*, *Salix* sp.), bet mazāks sūnu sugu skaits – uz "skābajiem" kokiem (*Alnus glutinosa*, *Betula pendula*, *Picea abies*). Koka diametrs, vecums, un attālums līdz nogāzes augšdaļai maz ietekmēja epifītisko sūnu izplatību. Visvairāk sūnu sugas (ietverot signālsugas) bija izplatītas uz koka stumbra līdz 0,5 m augstumam dienvidu debespusē, kā arī stumbra augšpusē uz slīpiem kokiem (dienvidu debespusē uz kokiem ziemeļu nogāzē un austrumu debespusē – uz kokiem rietumu nogāzē).