

This manuscript is contextually identical with the published paper:

Ódor, P. and van Hees, A.F.M. 2004. Preferences of dead wood inhabiting bryophytes for decay stage, log size and habitat types in Hungarian beech forests. *Journal of Bryology* 26: 79-95.

Preferences of dead wood inhabiting bryophytes to decay phase, log size and habitat types in Hungarian beech forests

PÉTER ÓDOR¹, and AD F. M. VAN HEES²,

1: Department of Plant Taxonomy and Ecology, Loránd Eötvös University, H-1117 Budapest, Pázmány Péter sétány 1/C. Hungary, e-mail: odor@ramet.elte.hu

2: ALTERRA, P.O.box 47, 6700 AA Wageningen, The Netherlands, e-mail: A.F.M.vanHees@Alterra.wag-ur.nl

KEYWORDS: bryophytes, dead wood, succession, generalised linear model

SUMMARY: This quantitative study describes the preference of bryophytes for certain decay phases in dead wood. The effects of habitat type (zonal versus ravine-like near-natural beech stands) and log size have been included in this study. Species preferences are analysed with a logistic regression model. A total of 30 bryophyte species were included in the analysis.

The species pool differs between habitat types. In the ravine-like forests more species are found and regionally rare epixylic species (mainly liverworts) are limited to these forests. In the ravine-like forests the species richness of the individual logs is higher than in the zonal forests and a larger proportion of logs is colonised by bryophytes. Even thin branches are more frequently colonised in ravine-like forests.

The species were classified into four categories on the basis of their preference to decay phases. The following categories were identified: epixylics, indifferent species, wide tolerant epixylics and epiphytes. The epixylics and wide tolerant epixylics prefer the latest decay phases. Wide tolerant epixylic species more often occur in earlier decay phases than do epixylics. The more common epixylic species have a wider tolerance to decay than do rare ones. Indifferent species and wide tolerant epixylics are regionally common bryophytes, and they often grow on substrates other than dead wood. Generally the probability of occurrence of these species increases with log size, but its effects is more important in zonal stands than in ravines.

Based on observed species responses a simplified scheme for bryophyte succession on dead wood has been developed.

INTRODUCTION

A major feature of unmanaged old-growth forests in the temperate region is the high amount of dead wood (Peterken, 1996). The amount of dead wood can be 10-15 times larger than in managed boreal spruce forests (Jonsson, 2000, Andersson & Hytteborn, 1991, Lesica et al., 1991) and 4-5 times larger than in managed temperate broad-leaved forests (Ódor & Standovár, 2001, Green & Peterken, 1997, Kirby et al. 1997). Unmanaged and managed forests differ considerably in the quality of dead wood (Söderström, 1988a, Jonsson, 2000, Kruys et al., 1999, Ódor & Standovár, 2001, Andersson & Hytteborn, 1991, Rambo & Muir, 1998). In old-growth forests the proportion of large logs and snags is high, the distribution of decay stages is more even and logs of different sizes and decay phases are continuously present in time. Whereas in managed stands the proportion of fine woody debris (small branches and logs) and stumps is high, well-decayed logs are under represented and the presence of dead wood depends mainly on forestry activities.

Dead wood is an important component of the forest ecosystem. In boreal forests tree regeneration is facilitated by nurse logs (Samuelsson, Gustafsson & Ingelög, 1994; Harmon et al., 1986; Esseen et al., 1997; Hofgaard, 1993) and in some flood-plain forests dead wood is a unique habitat for herbs (Dennis & Batson, 1974). Dead wood plays an important role in nutrient cycling and geomorphologic processes in forests and forest streams (Harmon et al., 1986). Perhaps the most important feature of dead wood is that thousands of species (eg. fungi, bryophytes, lichens, invertebrates, amphibians, cavity nesting birds, small mammals, bats) need dead wood as living, breeding and nesting site, and the survival of their populations may depend on the quantity and quality of dead wood. The importance of dead wood for different organisms has been reviewed for different parts of temperate region (Harmon et al., 1986; Maser and Trappe, 1984; Esseen et al., 1997; Samuelsson et al., 1994; Ferris-Kaan et al., 1993; Csóka, 2000; Eckloff & Ziegler, 1991).

Among bryophytes a lot of species are obligatory dead wood species (true epixylics) or facultative dead wood species (epiphytes, terricolous and rupicolous species). From the Hungarian bryoflora 11% occur mainly on dead wood (based on Orbán & Vajda, 1985) and in the Ariesului mic basin (Romania) 106 bryophytes were found on dead wood (Goia & Schumacher, 2000). In a study of 200 dead beech trees in two old-growth beech-fir forests in Slovenia 102 bryophytes were found on dead wood (Ódor

& van Dort, unpublished data). Generally, the importance of dead wood for bryophytes has been addressed by comparison of managed and unmanaged stands (e.g. Lesica et al., 1991; Gustafsson & Hallingbäck, 1988; Andersson & Hytteborn, 1991; Söderström, 1988a; Ódor & Standovár, 2001; Rambo & Muir, 1998). These studies came to a common conclusion: a group of obligate epixylics, predominantly liverworts, only can survive in remnants of natural stands. These species need a continuous presence of large logs of medium and late decay and a constant high air humidity: conditions that are usually missing in managed stands. In boreal stands the differences between managed and unmanaged stands are less pronounced. At the stand level indices for bryophyte species richness and diversity and the dominance of terricolous species are the same (Lesica et al., 1991, Gustafsson & Hallingbäck, 1988). Only on individual logs species richness is much higher in natural stands than in managed stands and there are clear differences in species composition (Andersson & Hytteborn, 1991, Lesica et al., 1991). In Hungary the natural beech stands differ from the managed ones mainly in the number of epixylic species, and the abundance-dominance distribution of species (Ódor & Standovár, 2001). A high amount of dead wood could also increase the diversity of rupicolous bryophyte communities (Ódor & Standovár 2002).

On a European scale the potential bryophyte vegetation on logs (the species pool) is predominantly connected to the major vegetation zones (Barkman, 1958, Phillippi, 1965, Hübschmann, 1986, Marstaller, 1986) and thus climate determined. In British Columbia the geographical distribution of most of the epixylic species is limited to one biogeoclimatic zone only (Qian, Klinka & Song, 1999). From regional studies it is evident that, in dead wood rich habitats, moisture condition (mainly air humidity) is the important factor determining species composition. In more humid forests the species richness and the abundance of hepatic species is higher than in dry forests. In dry forests the species richness is low and pleurocarp mosses and lichens dominate the cryptogamic vegetation (Raschendorfer, 1949, Muhle & LeBlanc, 1975, McCullough, 1948, Barkman, 1958). Despite the climatic and edaphic induced differences, all studies on dead wood and bryophytes show a compositional change with a change in decay phase (Muhle & Leblanc, 1975, Cornelissen & Karssemeier, 1987, Fehér & Orbán, 1981 Söderström, 1988b, Rambo & Muir, 1998, McCullough, 1948, Krusys et al., 1999).

Although the importance of dead wood for the diversity of bryophytes is evident, the species-specific preference for dead wood and the shift in dominance during succession is not always clear. In the temperate broad-leaved region most of the bryological studies on dead wood follow the synusial concept of vegetation (Barkman, 1973). Different systems of hierarchical classification with each a large number of epixylic communities are developed (Barkman, 1958; Hübschmann, 1986; Marstaller, 1986). The habitat preference of each community is described in terms of geographical area, edaphic conditions, naturalness and dead wood characteristics, although not always equally consistent. This complexity makes it difficult to derive detailed information on the ecological behaviour of bryophyte species growing on dead wood. Based on studies in coniferous forests Stefureac (1969) and Söderström (1988b) classified the bryophytes on dead wood in four categories, which reflect their preference to different decay phases: epiphyton-corticol, epixylic, sapro-lignicol and humicol-terricol species (sensu Stefureac, 1969) or epiphyte, early epixylic, late epixylic, and ground flora species (sensu Söderström, 1988b). It is not clear if this classification can be transferred directly to beech forests as litter accumulates on the forest floor and a well-developed terrestrial bryophyte layer is missing.

Several studies have addressed the importance of log size for species composition and species richness of dead wood (Söderström, 1988b, Rambo & Muir 1998, Kruys & Jonsson, 1999, Kruys et al., 1999, Ódor & Standovár, 2001). Generally, epixylic species are restricted to large logs (mainly epixylic hepatics). Small logs and branches decay rapidly and are easily covered by litter and overgrown by terrestrial species. These small logs and branches are only for a short period a suitable habitat for epixylic species. Furthermore a number of epixylic species have a low dispersal capacity, which limits the probability of colonising these small logs and branches (Söderström & Jonsson, 1992, Söderström & Herben, 1997, Söderström, 1990).

This study focuses on dead wood and bryophytes in four natural beech forests in Hungary. Two of the beech forests represent the zonal beech forests. The other two beech forests represent the ravine-like beech forests, with a high air humidity. Our objective is to characterise the preference of bryophyte species for different decay phases of the dead wood and the size of the dead wood, taking into account differences in local climate.

MATERIAL AND METHODS

Study Areas

The study was carried out in four near natural forest stands dominated by beech (*Fagus sylvatica* L.) (Fig. 1). All investigated stands are strict forest reserves. The stands have a heterogeneous stand structure and high amount of dead wood with a large variation in size and decay phases. Two selected sites are situated on a plateau and classified as zonal beech forest. One site is selected on a steep slope and one in a deep north-facing valley. Both sites are classified as ravine-like beech forests. The major differences between the zonal stands (Tátika and Óserdő) and the ravine-like stands (Kékes and Leány) are related to:

- Microclimate: ravine-like stands are colder and rarely have an air humidity below 80%;
- Density of coarse woody debris: higher in ravine-like stands; 290 m³/ha versus 138 m³/ha (Ódor, unpublished data; Ódor & Standovár, 2001);
- Abundance of co-occurring tree species, both living and dead: high abundance of sycamore (*Acer pseudoplatanus* L.), witch elm (*Ulmus glabra* L.), lime (*Tilia platyphyllos* L.) in the ravine-like stands.

Tátika lies in the southwest of Hungary near the lake Balaton. It is a zonal beech forest situated on a basalt plateau (600 m a.s.l) with a mean annual precipitation of 720 mm and a mean annual temperature of 9.7 °C. The stand is more than 200 years old and has been harvested in the past. The last 100 years it has been free of management activities. Beech dominates the stand, with hornbeam (*Carpinus betulus* L.) and common maple (*Acer campestre* L.) as co-dominant species. The soil is a relatively deep, nutrient rich, brown forest soil. In the shrub layer *Sambucus nigra* L. is important. In spring the herb layer is dominated by geophytes (eg. *Allium ursinum* L.), in summer by *Urtica dioica* L.

The three other stands are located in the northern part of Hungary and they have a similar continental montane climate (800 m a.s.l., annual precipitation between 800 and 900 mm and mean annual temperature is 5.5-6.5 °C).

Kékes Forest Reserve is located in the Mátra mountains on a steep north facing slope of the peak Kékes. The bedrock is andesite, with a nutrient poor, shallow, brown forest soil. Because of the steepness of the slopes, scree slopes and rock outcrops are

common. The stand has never been cut. It has a heterogeneous structure with different development phases, including gaps and regeneration patches (Czajlik, 1996). The age of oldest trees is more than 250 yr. This study is concentrated on a scree slope, with a special ravine-like microclimate (air humidity between 80 and 90%). The beech forest has an open canopy with large gaps. Beech is dominating with sycamore, lime and witch elm as co-dominant species. The surface is covered with large andesite rocks, with a thin, nutrient rich forest soil mixed with decayed woody material among the rocks. The shrub and herb layer is well developed, the most common species are *Sambucus racemosa* L., *Solanum dulcamara* L., *Urtica dioica*, *Impatiens noli-tangere* L. and *Athyrium filix-femina* (L.) Roth. The moss layer has a high cover and is species rich (Odor, 2000, Odor & Standovar, 2001, Odor & Standovar 2002).

Oserdo Forest Reserve is a 25 ha large zonal beech stand situated on the plateau of Bukk mountains. The bedrock is limestone, the soil is a medium deep brown forest soil. The topography is flat with locally small dolinas. The stand has been managed and cut in the past. However, the last 60 years it has been free of management activities. The ages of the dominant beech trees vary between 150-250 yr. This stand also has a heterogeneous structure with trees of different sizes, canopy gaps and regeneration patches. The shrub layer is nearly absent, but the forest floor is covered with carpets of herbs dominated by *Galium odoratum* (L.) Scop., *Glechoma hederacea* L. and *Hordelymus europaeus* (L.) C. O. Harz.

Leany Forest Reserve is situated also in Bukk mountains and it is close to Oserdo. The reserve Leany lies in a deep north-facing valley surrounded by 50-70 year old beech stands and rocks faces. The bedrock is limestone, between the rock outcrops the soil is a very shallow rendzina soil. The tree canopy is open, beech dominates and sycamore and witch elm are co-dominant. *Parietalia officinalis* L., *Athyrium filix-femina* and *Chrysosplenium alternifolium* L. are the most important species in the dense herb layer. Bryophytes are abundant, both on rocks and on dead wood.

Data collection

The density of dead wood and their size and decay phase differed between the four selected beech stands. To include sufficient variation in decay phases and an approximately equal number of large pieces of dead wood in the analysis, the size of

the sample plot varied. The plot size was 1000 m² in Óserdő, 800 m² in Tátika and 400 m² in Kékes and Leány.

In each plot all pieces of dead wood with the largest diameter > 5 cm and a minimum length of 0.5 m (hereafter referred to as logs) were included in this study. Each log was described by its dominant decay phase, its length and by one to eight diameters, the number depending on the length of the log. Length and average diameter were used to calculate the log volume. Decay phase was an ordinal variable ranging from 1 to 6. The classification by decay phase was based on the cover of the bark, the presence of twigs and branches, the softness of the wood, surface characteristics of the log and the log shape (see Table 1). This system of decay phases was a modification of the systems used by McCullough (1948), Söderström (1988b) and Hofgaard (1993).

In well-decayed logs it was impossible to determine the species. Thus species information was only available for the early decay phases. Consequently information on tree species was excluded from the analysis.

Presence/absence data of bryophyte species were recorded for all logs. As the differences between *Plagiothecium* species are difficult to identify in the field, these species were classified at the genus level. Laboratory analysis showed that most of the specimens were *P. denticulatum* or *P. nemorale*.

Nomenclature followed Corley et al. (1981) and Corley & Crundwell (1991) for mosses and Grolle (1983) for liverworts. In the figures abbreviations of species names were used. This abbreviation was based on the first three letters of the genus and the species names.

Data analysis

Analysis of site-specific differences in species composition was based on the relative frequency of the species per site, using average linkage as hierarchical agglomerative clustering techniques (SYN-TAX 2000; Podani, 2001). The euclidean distance was chosen as the distance function in this analysis (Podani, 2000). The compositional differences between sites were demonstrated with constrained block clustering (Podani & Feoli, 1991; SYN-TAX 5.0, Podani, 1993). The number of blocks was set to 6 and the initial clustering was based on field experience. Only species occurring more than once in the four sites studied were included in the cluster procedure.

The presence/absence of bryophytes was analysed with a logistic regression model (McCullagh & Nelder, 1983). This model predicted the probability to find a certain bryophyte on a certain log. Predictor variables to be tested in the analysis were site, volume and decay phase. Preliminary analysis indicated that the effect of volume and decay phase might differ between sites. Consequently these interaction terms were included in the analysis as well. The maximum model to be tested was:

$$\ln(p/(1-p)) = C + C_{dp} + C_v * V + C_s + C_{dp,s} + C_{v,s} * V + \varepsilon \quad <1>$$

with p probability of occurrence of a species (value between 0 and 1)
V Volume in m³
C regression constant
C_{dp} regression constant for decay phase (6 levels)
C_v regression constant for volume
C_s regression constant for site (4 levels)
C_{dp,s} regression constant for site.decay (4*6 levels)
C_{v,s} regression constant for site.volume (4 levels)
ε residual error of regression

Model selection was based on forward selection. Variables were only included in the model if they significantly improved the goodness of fit of the original model. The order of variables to be included was the same as in model 1. The analysis and predictions were made with Genstat 4.2 (Payne and Arnold, 2000). Species occurring on more than 15 logs in the whole data set were included in the analysis. Only 30 out of 75 species met this criterion.

To characterise the effects of decay and volume different sets of graphs are presented. Probabilities of occurrence per decay phase are presented by bar graphs. For species with a significant effect of volume predictions are based on a volume of 0.5 m³. The effects of volume are presented by line graphs. For epixylic species the predicted effects of volume are averaged over the decay phases 4 to 6, for indifferent species 1 to 6 and for epixylic species with a wide tolerance 3 to 6, respectively. For epiphytes predictions are given for decay phase 1.

RESULTS

Sites

General differences in bryophyte richness are present in Table 2. In the zonal stands, Tátika and Óserdő, larger proportions of logs are found without bryophytes than in the ravine-like stands, Kékes and Leány. A re-examination of the data indicates that in the zonal stands thin logs (diameter between 5-10 cm) are not colonised by bryophytes, while in the ravine stands these thin logs are already colonised. The ravine-like stand Leány is the most species rich site, with 51 species. The number of species in the other three sites varies between 31 and 39. Looking at the average number of species per log it is clear that both ravine-like sites have the most species rich logs.

The hierarchical cluster analysis (Fig. 2) and block cluster analysis (Table 3) show that the ravine-like stands Leány and Kékes on the one hand and the zonal stand Tátika on the other hand strongly differ in their species composition, while the zonal stand Óserdő holds an intermediate position. The ravine-like stands Leány and Kékes are characterised by the species from block 4 to 6 (Table 3). Block 4 is common to both ravine stands. Species from block 5 are more common in Kékes and species from block 6 are almost restricted to Leány. Most of the species in block 4 and 6 are epixylic species, including rare species such as *Buxbaumia viridis*, *Lophozia ascendens*, *Nowellia curvifolia*, *Blepharostoma trichophyllum*, *Riccardia palmata* and *Chiloschyphus pallescens*. These species live exclusively on well-decayed logs. Some species from block 5 grow on andesite rocks but can grow on dead wood as an alternative substrate. The zonal site Tátika is characterised by species from block 2, most of them are epiphytes. The second zonal site Óserdő is not characterised by a specific group of species. It has species from group 3 in common with the two ravine sites. Species preferences to specific sites have been tested with logistic regression. The results of this analysis are included in Table 3. For 28 out of 30 species the effect of sites were (highly) significant. The logistic regression yielded for site effects similar results as block cluster analysis.

The reserves Leány, Kékes and Óserdő are located in the same mountain chain with similar regional climatic conditions, while the reserve Tátika is located in another geographic region with a somewhat warmer and drier climate. Although the reserves Leány and Óserdő are situated close to each other (distance < 2 km) and have the

same parent material (limestone) the species composition of Leány is more similar to Kékes (parent material andesite) than to Óserdő. Leány and Kékes are both ravine-like forests with a relatively cool local climate and high air humidity.

Decay phases and volume

An overview of the significance and estimated parameter values of the factors analysed with the logistic regression model is presented in Table 4. Based on graphical interpretation of the fitted logistic regression model, the 30 species studied were classified into the following four groups in accordance to their preference to decay phases: epixylics, epixylics with a wide tolerance, indifferent species and epiphytes (Fig. 3-10).

Epixylic species: *Rhizomnium punctatum*, *Herzogiella seligeri*, *Plagiomnium cuspidatum*, *Plagiothecium species*, *Amblystegium riparium*, *Lophocolea minor*, *Plagiochila porelloides*, *Blepharostoma trichophyllum*, *Riccardia palmata*, *Nowellia curvifolia*, *Chylosciphus pallescens*.

The largest group is the group of epixylic species, with 11 out of 30 species (Fig. 3). The probability of occurrence of these species is relatively low in early decay phases (1 and 2) and increases in later decay phase. They have an optimum in decay phase 4 to 6. The response of epixylic species to decay phase differs between ravine sites and zonal sites, probably reflecting differences in air humidity. In zonal sites less epixylic species and mostly common epixylic species are found and their occurrence is almost restricted to the later stages of decay (*Rhizomnium punctatum*, *Herzogiella seligeri*, *Plagiomnium cuspidatum*, *Plagiothecium species*). In the ravine-like sites more epixylic species were found, both common and rare species. In comparison to zonal sites, *Rhizomnium punctatum*, *Herzogiella seligeri* are more frequent in ravine sites on logs with an early decay phase. Also under ravine-like conditions some epixylic species can grow on substrate types such as soil or rocks (*Rhizomnium punctatum*, *Plagiomnium cuspidatum*, *Plagiothecium species*, *Amblystegium riparium*, *Lophocolea minor*, *Plagiochila porelloides*).

For six out of eleven epixylic species a positive effect of volume on the probability of occurrence was observed (*Rhizomnium punctatum*, *Herzogiella seligeri*, *Plagiomnium*

cuspidatum, *Amblystegium riparium*, *Lophocolea minor*, *Nowellia curvifolia*, Fig. 4). The effect of volume is less pronounced in ravine-like stands than in zonal stands.

Indifferent species: *Hypnum cupressiforme*, *Bryum subelegans*, *Pseudoleskeella nervosa*, *Pterigynandrum filiforme*, *Platygyrium repens*, *Plagiomnium rostratum*, *Homalothecium sericeum*, *Metzgeria furcata*, *Isothecium alopecuroides*.

Species are classified as indifferent when: (1) the effect of decay phase was not significant (*Pseudoleskeella nervosa*, *Pterigynandrum filiforme*, *Plagiomnium rostratum*, *Homalothecium sericeum*, *Metzgeria furcata*); (2) the effect of decay phase is significant but small (*Hypnum cupressiforme*, *Platygyrium repens*, Fig. 5); (3) there is no clear trend in the preference for decay phases (*Bryum subelegans*, *Isothecium alopecuroides*, Fig. 5). These types of response indicate that these species have no clear preference for early, intermediate or late decay phases. Both common and rare species are present in this group.

Fieldwork indicated that *Pseudoleskeella nervosa*, *Pterigynandrum filiforme*, *Platygyrium repens*, *Homalothecium sericeum* and *Metzgeria furcata* were more common in early decay phases. However, these epiphytes can survive with a low abundance in later decay phases on isolated bark remnants and on spots of hard wood. Consequently the analysis of the presence/absence data does not show any preference for early decay phases.

For seven out of nine indifferent species the effect of volume on the probability of occurrence was significant (Fig. 6), still it was not significant for *Plagiomnium rostratum* and *Isothecium alopecuroides*. *Hypnum cupressiforme*, the most common species reached the maximum probability of occurrence ($p=1$) at a low volume of 0.1 m³ in Kékes and at 0.4 m³ in other sites.

Epixylic species with a wide tolerance: *Lophocolea heterophylla*, *Brachythecium velutinum*, *Amblystegium serpens*, *Brachythecium rutabulum*, *Brachythecium salebrosum*, *Sanionia uncinata*, *Dicranum scoparium*.

Species classified into this group have an optimum in occurrence in later decay phases but are also frequently found on logs with early decay phases (*Lophocolea heterophylla*, *Amblystegium serpens*, *Sanionia uncinata*, *Dicranum scoparium*, Fig. 7). Species that behave as indifferent in the ravine-like stands but as epixylic species in the zonal stands are also included in this group (*Brachythecium velutinum*,

Brachythecium rutabulum, *Brachythecium salebrosum*). Generally, epixylic species with a wide tolerance are common in the four sites studied. Only *Sanionia uncinata* and *Dicranum scoparium* are restricted to the ravine sites, but here they are common as well.

Volume has a positive effect on the occurrence of all epixylic species with a wide tolerance (Fig. 8). However this effect is more pronounced in zonal stands than in ravines for *Lophocolea heterophylla*, *Brachythecium velutinum*, *Brachythecium rutabulum*, *Brachythecium salebrosum*.

Epiphyte species: *Leucodon sciuroides*, *Orthotrichum stramineum*, *Frullania dilatata*.

The occurrence of epiphyte species is restricted to the bark of the logs. The probabilities of occurrence are high in decay phase 1, low in 2 and 3 and very low in later phases (Fig. 9). *Leucodon sciuroides* and *Frullania dilatata* are predominantly found in Tátika.

Volume has large effect on the occurrence of these species (Fig. 10), especially on *Leucodon sciuroides* and *Frullania dilatata*.

DISCUSSION

Succession

The logistic regression model predicts the probability of occurrence of bryophyte species on beech logs as a function of decay phase, volume and site. Classifying the responses of individual species to decay phase it is possible to visualise the succession of bryophytes on beech logs in the Central-European beech forests (Fig. 11). During decomposition process the outer surface of the log is changing (bark → hard wood → soft wood → fully decomposed wood), which results in a compositional change in the bryophyte community. Although it was not analysed in this study the cover of bryophytes increases during the first part of this process, it reaches its maximum at decay phase 3 or 4 and it decreases in decay phases 5 and 6. The compositional change is unidirectional, as the influence of the bryophyte cover on the decomposition process is negligible. This is an essential difference with the succession of fungi

communities. Here, the fungi species can determine the process of decay, and thus the abiotic condition of the log (Boddy, 2001, Heilmann-Clausen, 2001). Consequently, the type of fungal induced decay can influence the succession of bryophytes. For instance, if the decomposition process is modified by some *Pyrenomycetes* species the well-decayed wood will become so dry, that the epixylic species are not able to colonise or to survive.

The succession of bryophytes on beech logs is a typical example of degradative succession (Begon, Harper & Townsend, 1996). The first colonisers of the beech logs are indifferent species and epiphytes. In the Central-European climate the occurrence of epiphytes on living beech trees is restricted to the stem base (upto 0.5-1 m in height). The major part of log is colonised by epiphytes after the tree has fallen. As colonisation is the first important process, the succession of bryophytes on beech logs could be considered as primary succession (Crawley, 1986). In the investigated sites there is a clear compositional change with a change in decay phase. However, the species pool (the potential vegetation on logs) differed between the sites as this pool is determined by climatic factors, even on this geographically small scale. In zonal stands the bryophyte vegetation on well-decayed logs is poor in species. The logs are colonised by indifferent species and epixylics with a wide tolerance. From the epixylic species only the most common ones are present (*Rhizomnium punctatum*, *Herzogiella seligeri*, *Plagiomnium cuspidatum*, *Plagiothecium spp.*). In the more humid ravine-like beech forests regionally rare obligate epixylic liverworts are found on beech logs (*Blepharostoma trichophyllum*, *Riccardia palmata*, *Nowellia curvifolia*, *Calypogeia suecica*, *Chyloschyphus pallescens*, *Lophozia ascendens*). In the boreal region species-rich epixylic vegetation dominated by liverworts is characteristic for old-growth and near-natural stands (Andersson and Hytteborn, 1991, Gustafsson & Hallingbäck, 1988, Lesica et al., 1991, Rambo & Muir, 1998, Söderström, 1988a). In Hungary the present distribution of obligate epixylic liverworts is restricted to small remnants of near natural beech forests in ravine-like conditions, indicating the importance of local climatic conditions. In the remnants of near natural beech forests under zonal conditions, these species are absent. However in natural forest landscapes the presence of these species can be expected under zonal conditions (Söderström, 1989, Söderström & Jonsson, 1992). Apparently forest fragmentation has led to local extinction of obligate epixylic liverworts. Most of the indifferent species and epixylic species with a wide tolerance are found in all sites. The few species in these two

groups, with a clear preference for ravine-like conditions, mainly live on rocks and use logs as a suboptimal substrate (e.g. *Dicranum scoparium*, *Isothecium alopecuroides*, *Plagiomnium rostratum*).

Aude & Lawesson (1998) and Aude & Poulsen (2000) have shown for managed Danish beech forests that the species-richness of the epiphyte vegetation primarily is related to stand structure (proportion of large trees, multi-layered canopy and heterogeneous light conditions). We expect that under Central-European conditions these are also the main stand characteristics determining species-richness of epiphytes. The relevance of local climate for epiphytes is not evident from this study, as epiphyte species did not have a preference for the humid ravine-like stands. On the other hand micro-climatic conditions might be important, as is indicated by the difference in epiphyte abundance on standing and fallen trees. The bark of the standing trees is more susceptible to drought and thus colonisation is more difficult than on the bark of fallen trees. Although the tree species of the logs was excluded from this study, we expect that it might have influenced the epiphyte composition of the logs. The more rough and nutrient-rich bark of trees species as sycamore, ash and lime provide more favourable habitat for epiphytes than the smooth and nutrient-poor bark of beech (Barkman, 1958, Slack, 1976, Rasmussen, 1975). The differences between these tree species could be less important in later phases of decay.

There is a clear relation between the general ecological classification of the bryophytes by their preferences for certain decay phases and species frequency. In this study most of the indifferent and epixylic species with a wide tolerance were common, both at a regional scale and local scale. Exceptions are *Sanionia uncinata* and *Dicranum scoparium*, which have a preference for ravine-like stands. Their wide ecological amplitude in relation to decay and log size could explain the high frequency of this species. Further more these species are not restricted to dead wood but grow on other substrates (rocks, soil). This gives these species an advantage in colonising dead wood. Concentrating on epixylic species we found that the more common species are less specific for later decay phases (from decay phase 3 to 6) than are the rare epixylic species. Common epixylics (e.g. *Rhizomnium punctatum*, *Herzogiella seligeri*) have a relatively high probability of occurrence in decay phase 1 and 2 (0.2-0.4), while for rare species (*Lophocolea minor*, *Blepharostoma trichophyllum*, *Riccardia palmata*) these probabilities are close to zero in the same sites. There are two possible explanations: (1) the ecological amplitude for decay is

wider for more frequent species and this explains why these species are more common; (2) the reason of their higher frequency lies in a high reproductive ability or high dispersal capacity and the observed wider ecological amplitude is the outcome of the stochastic process of colonisation.

Although the succession model indicates an unidirectional compositional change in log inhabiting bryophyte vegetation, its dynamic is not clear yet. Because the outer surface of logs is continuously renewed, this compositional change do not take place in a permanently existing bryophyte layer, but is the result of extinction and colonisation of species. Most of the autoecological studies dealing with epixylic liverworts do not measure the extinction and colonisation of populations directly. However, the high growth rate, sexual and asexual reproductive allocation, and aggregated pattern of patches indirectly show a very high rate of extinction and colonisation (Jonsson & Söderström, 1988a, Söderström & Jonsson, 1989, Laaka-Lindberg, 1999, Laaka-Lindberg & Heino, 2001). Kimmerer (1993) investigating the change in ecological status of *Tetraxis pellucida* patches (asexual, sexual, senescent, disturbed, competing) demonstrated that 40% of patches changed their status after 1 year.

The different strategies of bryophyte species during succession are not yet clear. It is supposed that slow growing liverworts and acrocarp mosses can colonise gaps of the intact moss cover and on open wood patches (Kimmerer & Young, 1996), while fast growing pleurocarp mosses will build large patches in a short time.

We found that species composition and the relative abundance of the species on logs with similar conditions (site, decay phase, size) could differ considerably. We expect that the actual species composition depends on the disturbance history of logs and the stochastic events of colonisation and extinction. For gametophytes the importance of interspecific competition is less important (Söderström, 1988c, During, 1987), although its effect could be considerable at protonema level during colonisation (Watson 1980).

Effects of log size

Generally log size has a positive effect on the occurrence of bryophytes. The effect of log size (in this case expressed by volume) differed between zonal and ravine-like sites. It was a significant factor for nearly all the species in zonal stands (except

Plagiothecium species). Log size was not important only for a few species limited to ravine-like conditions (*Blepharostoma trichophyllum*, *Riccardia palmata*, *Isothecium alopecuroides*, *Plagiomnium rostratum*). For species occurring in both site types, the effect of log size is often more pronounced in zonal stands as compared to ravine-like stands (*Rhizomnium punctatum*, *Brachythecium velutinum*, *Brachythecium rutabulum*). This positive effect of log size on the probability of occurrence indicates that large logs have more species than small logs. However, rare species had to be excluded from the analysis (not enough data). Consequently the results of this logistic regression analyses can not be used to predict the bryophyte richness of a log in investigated sites. At the same time this study showed that common species had a high probability of occurrence on small logs. This leads to the conclusion that the bryophyte flora on small logs is species-poor and dominated by common species while on large logs the bryophyte flora is species-rich and rare species might be present. The importance of large logs for bryophyte diversity has been confirmed by studies comparing old-growth forests and managed forests (Lesica et al., 1991, Gustafsson & Hallingbäck, 1988, Andersson & Hytteborn, 1991, Söderström, 1988a, Ódor & Standovár, 2001, Rambo & Muir, 1998). However, if the amount of dead wood is very low, as in managed forests, the importance of small woody debris (branches etc.) shouldn't be neglected. Studies by Kruys & Jonsson (1999) and Ódor & Standovár (2001) have shown that a large number of thin logs and branches yield a higher bryophyte diversity than a few large logs.

In the boreal region the fast-growing, competitive terricolous bryophytes (*Hylocomium splendens*, *Pleurozium schreberi*) overgrow the epixylic species, which explains why epixylics are missing on thin logs (Söderström, 1988b). In the zonal beech forests epixylic species are missing on thin logs as these logs are rapidly buried by dead leaves and are incorporated in the humus layer before they can reach a stage of decay suitable for the colonisation by epixylic species. However in ravine-like stands epixylic species are present on thin logs. Here the thin logs will fall on small and large boulders and stay free from the soil. Consequently the log will not be buried and epixylic species are able to colonise these logs and at the same time the competitive ability of rupicolous species is not large enough to overgrow them.

ACKNOWLEDGEMENTS

The authors are especially grateful to Tibor Standovár who helped developing the methodology and improving the manuscript. Many thanks are due to Erzsébet Szurdoki, Beáta Papp and Peter Erzberger who helped at field work and bryophyte identification. The study was supported by grant OTKA F029762, OTKA F21300, the EU 5th Framework Programme Nat-Man (QLRT1-CT99-1349) and an IAC fellowship facilitated for the first author to work in ALTERRA on this study.

REFERENCES

- Andersson LI, Hytteborn H. 1991.** Bryophytes and decaying wood - a comparison between managed and natural forest. *Holarctic Ecology* **14**: 121-130.
- Aude E, Lawesson JE. 1998.** Vegetation in Danish beech forest: the importance of soil, microclimate and management factors, evaluated by variation partitioning. *Plant Ecology* **134**: 53-65.
- Aude E, Poulsen RS. 2000.** Influence of management on the species composition of epiphytic cryptogams in Danish Fagus forest. *Applied Vegetation Science* **3**: 81-88.
- Barkman JJ. 1973.** Synusial approaches to classification. In: Whittaker RH, ed. *Ordination and classification of communities*. The Hague: Dr. W. Junk Publishers, 435-492.
- Barkman JJ. 1958.** *Phytosociology and ecology of cryptogamic epiphytes*. Assen: Van Gorcum.
- Begon M, Harper JL, Townsend CR. 1996.** *Ecology. Individuals, Populations and Communities*. Oxford: Blackwell Science Ltd.
- Boddy L. 2001.** Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. *Ecological Bulletins* **49**: 43-56.
- Corley MFV, Crundwell AC, Düll R, Hill MO, Smith AJE. 1981.** Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. *Journal of Bryology* **11**: 609-689.

- Corley MFV, Crundwell AC. 1991.** Additions and amendments to the mosses of Europe and the Azores. *Journal of Bryology* **16**: 337-356.
- Cornelissen JHC, Karssemeijer GJ. 1987.** Bryophyte vegetation on spruce stumps in the Hautes-Fagnes, Belgium, with special reference to wood decay. *Phytocoenologia* **15**: 485-504.
- Crawley MJ. 1986.** The structure of plant communities. In: Crawley MJ, ed. *Plant Ecology*. Oxford: Balkwell Scientific Publications, 1-50.
- Csóka Gy. 2000.** Az elpusztult, korhadó fa szerepe az erdei biodiverzitás fenntartásában. In: Frank T, ed. *Természet - Erdő - Gazdálkodás*. Eger: Magyar Madártani és Természetvédelmi Egyesület, Pro Silva Hungaria Egyesület, 85-96.
- Czájlik P. 1996.** Koreloszlás és szukcesszió háborítatlan erdőállományokban: esettanulmány. In: Mátyás Cs, ed. *Erdészeti ökológia*. Budapest: Mezőgazdasági Kiadó, 84-92.
- Dennis WM, Batson WT. 1974.** The floating log and stump communities in the Santee Swamp of south Carolina. *Castanea* **39**: 166-170.
- During HJ, van Tooren BF. 1987.** Recent developments in bryophyte population ecology. *Trends in Evolution and Ecology* **2**: 89-93.
- Eckloff W, Ziegler W. 1991.** Über den Wert toter Bäume in der Waldlebensgemeinschaft. *Forstarchiv* **62**: 105-107.
- Esseen P-A, Ehnström B, Ericson L, Sjöberg K. 1997.** Boreal forests. *Ecological Bulletins* **46**: 16-47.
- Fehér G, Orbán S. 1981.** A bükki őserdő korhadó fáinak mohacönológiai vizsgálata. *Fol.Hist.-nat.Mus.Matr.* **7**: 15-28.
- Ferris-Kaan, R., Lonsdale, D., Winter, T. 1993.** *The conservation management of dead wood in forests*. Research Information Note 241. Research Publication Officer, The Forestry Authority, Research Division, Alice Holt Lodge.
- Goia I, Schumacker R. 2000.** Researches on the bryophytes from rotten wood in the Ariesului mic basin. *Contributii Botanice* **1**: 91-99.
- Green P, Peterken GF. 1997.** Variation in the amount of dead wood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. *Forest Ecology and Management* **98**: 229-238.
- Grolle R. 1983.** Hepatics of Europe including the Azores: an annotated list of species, with synonyms from the recent literature. *Journal of Bryology* **12**: 403-459.

- Gustafsson L, Hallingbäck T. 1988.** Bryophyte flora and vegetation of managed and virgin coniferous forest in South-West Sweden. *Biological Conservation* **44**: 283-300.
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW. 1986.** Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**: 133-276.
- Heilmann-Clausen J. 2001.** A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. *Mycological Research* **105**: 575-596.
- Hofgaard A. 1993.** Structure and regeneration pattern in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science* **4**: 601-608.
- Hübschmann A. 1986.** *Prodromus der Moosgesellschaften Zentraleuropas*. Berlin, Stuttgart: J. Cramer.
- Jonsson BG, Söderström L. 1988.** Growth and reproduction in the leafy hepatic *Ptilidium pulcherrimum* (G. Web.) Vainio during a 4-year period. *Journal of Bryology* **15**: 315-325.
- Jonsson BG. 2000.** Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* **11**: 51-56.
- Kimmerer RW. 1993.** Disturbance and dominance in *Tetraphis pellucida*: a model of disturbance frequency and reproductive mode. *The Bryologist* **96**: 73-79.
- Kimmerer RW, Young CC. 1996.** Effect of gap size and regeneration niche on species coexistence in bryophyte communities. *Bulletin of the Torrey Botanical Club* **123**: 16-24.
- Kirby KJ, Reid CM, Thomas RC, Goldsmith FB. 1997.** Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology* **35**: 148-155.
- Kruys N, Fries C, Jonsson BG, Lämäs T, Ståhl G. 1999.** Wood inhabiting cryptogams on dead norway spruce (*Picea abies*) trees in managed Swedish boreal forests. *Canadian Journal of Forest Research* **29**: 178-186.
- Kruys N, Jonsson BG. 1999.** Fine woody debris is important for species richness on logs in managed boreal spruce forests in northern Sweden. *Canadian Journal of Forest Research* **29**: 1295-1299.

- Laaka-Lindberg S. 1999.** Asexual reproduction in a population of a leafy hepatic species *Lophozia silvicola* Buch in central Norway. *Plant Ecology* **141**: 137-144.
- Laaka-Lindberg S, Heino M. 2001.** Clonal dynamics and evolution of dormancy in the leafy hepatic *Lophozia silvicola*. *Oikos* **94**: 525-532.
- Lesica P, McCune B, Cooper SV, Hong WS. 1991.** Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* **69**: 1745-1755.
- Marstaller R. 1986.** Die Moosgesellschaften auf morschem Holz und Rohhumus. *Gleditschia* **15**: 73-138.
- Maser C, Trappe JM. 1984.** *The seen and unseen world of the fallen tree*. Pacific Northwest Forest and Range Experiment Station, U.S.
- McCullagh P, Nelder JA. 1983.** *Generalized linear models*. London: Chapman and Hall Ltd.
- McCullough HA. 1948.** Plant succession on fallen logs in a virgin spruce-fir forest. *Ecology* **29**: 508-513.
- Muhle H, LeBlanc F. 1975.** Bryophyte and lichen succession on decaying logs. I. Analysis along an evaporational gradient in Eastern Canada. *Journal of Hattori Botanical Laboratory* **39**: 1-33.
- Orbán S, Vajda L. 1983.** *Bryophyte Flora of Hungary (in hungarian)*. Budapest: Akadémiai Kiadó.
- Ódor P. 2000.** Description of the bryoflora and bryophyte vegetation of Kékes North Forest Reserve in Mátra mountains (N-Hungary). *Kitaibelia* **5**: 115-123.
- Ódor P, Standovár T. 2001.** Richness of bryophyte vegetation in near-natural and managed beech stands: the effects of management-induced differences in dead wood. *Ecological Bulletins* **49**: 219-229.
- Ódor P, Standovár T. 2002.** Substrate specificity and community structure of bryophyte vegetation in a near-natural montane beech forests. *Community Ecology* **3**: 39-49.
- Payne RW, Arnold GM, eds. 2000.** *Genstat release 4.2 reference manual. Vol. I-III*. Oxford: VSN International.
- Peterken GF. 1996.** *Natural woodland. Ecology and conservation in northern temperate regions*. Cambridge: Cambridge University Press.

- Philippi G. 1965.** Moosgesellschaften der morschen Holzes und des Rohhumus in Schwarzwald, in der Rhön, im Weserbergland und im Harz. *Nova Hedwigia* **9**: 185-233.
- Podani J. 1993.** *SYN-TAX-pc Computer Programs for Multivariate Data Analysis in Ecology and Systematics. Version 5.0. User's Guide.* Budapest: Scientia Publishing.
- Podani J. 2000.** *Introduction to the exploration of multivariate biological data.* Leiden: Backhuys Publishers.
- Podani J. 2001.** *SYN-TAX 2000. Computer programs for data analysis in ecology and systematics. User's manual.* Budapest: Scientia Publishing.
- Podani J, Feoli E. 1991.** A general strategy for the simultaneous classification of variables and objects in ecological data tales. *Journal of Vegetation Science* **2**: 435-444.
- Qian H, Klinka K, Song X. 1999.** Cryptogams on decaying wood in old-growth forests on southern coastal British Columbia. *Journal of Vegetation Science* **10**: 883-894.
- Rambo TR, Muir PS. 1998.** Bryophyte species association with coarse woody debris and stand ages in Oregon. *The Bryologist* **101**: 366-376.
- Raschendorfer I. 1949.** Beobachtungen über die Besiedlung von modernem Holz mit besonderer Berücksichtigung der adnaten Vereine. *Österreichische Botanische Zeitschrift* **96**: 232-280.
- Rasmussen L. 1975.** The bryophytic epiphyte vegetation in the forest, slotved Skov, Northern Jutland. *Lindbergia* **3**: 15-38.
- Samuelsson J, Gustafsson L, Ingelög T. 1994.** *Dying and dead trees - a review of their importance for biodiversity.* Uppsala: Swedish Threatened Species Unit, Sw.Univ.of Agricult.Sci.
- Slack NG. 1976.** Host specificity of bryophytic epiphytes in eastern north America. *Journal of Hattori Botanical Laboratory* **41**: 107-132.
- Söderström L. 1988a.** The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in Northeast Sweden. *Biological Conservation* **45**: 169-178.
- Söderström L. 1988b.** Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic Journal of Botany* **8**: 89-97.

- Söderström L. 1988c.** Niche width and niche overlap in some epixylic bryophytes. In: Herben T, ed. *Proceedings of the sixth CEBWG Meeting*. Liblice, Czechoslovakia: 108-119.
- Söderström L. 1989.** Regional distribution patterns of bryophyte species on spruce logs in northern Sweden. *The Bryologist* **92**: 349-355.
- Söderström L, Jonsson BG. 1989.** Spatial pattern and dispersal in the leafy hepatic *Ptilidium pulcherrimum*. *Journal of Bryology* **15**: 793-802.
- Söderström L. 1990.** Dispersal and distribution patterns in patchy, temporary habitats. In: Krahulec F, ed. *Spatial processes in plant communities*. The Hague: SBP Publishers, 99-109.
- Söderström L, Jonsson BG. 1992.** Fragmentation of old-growth forests and bryophytes on temporary substrates. *Svensk Bot. Tidskr.* **86**: 185-198.
- Söderström L, Herben T. 1997.** Dynamics of bryophyte metapopulations. *Advances in Bryology* **6**: 205-240.
- Stefureac TI. 1969.** *Studii briologice in unele formatiuni de vegetatie din Romania*. Bucuresti: Acad. Repub. Soc. Romania.
- Watson MA. 1980.** Patterns of habitat occupation in mosses - relevance to considerations of the niche. *Bulletin of the Torrey Botanical Club* **107**: 346-372.

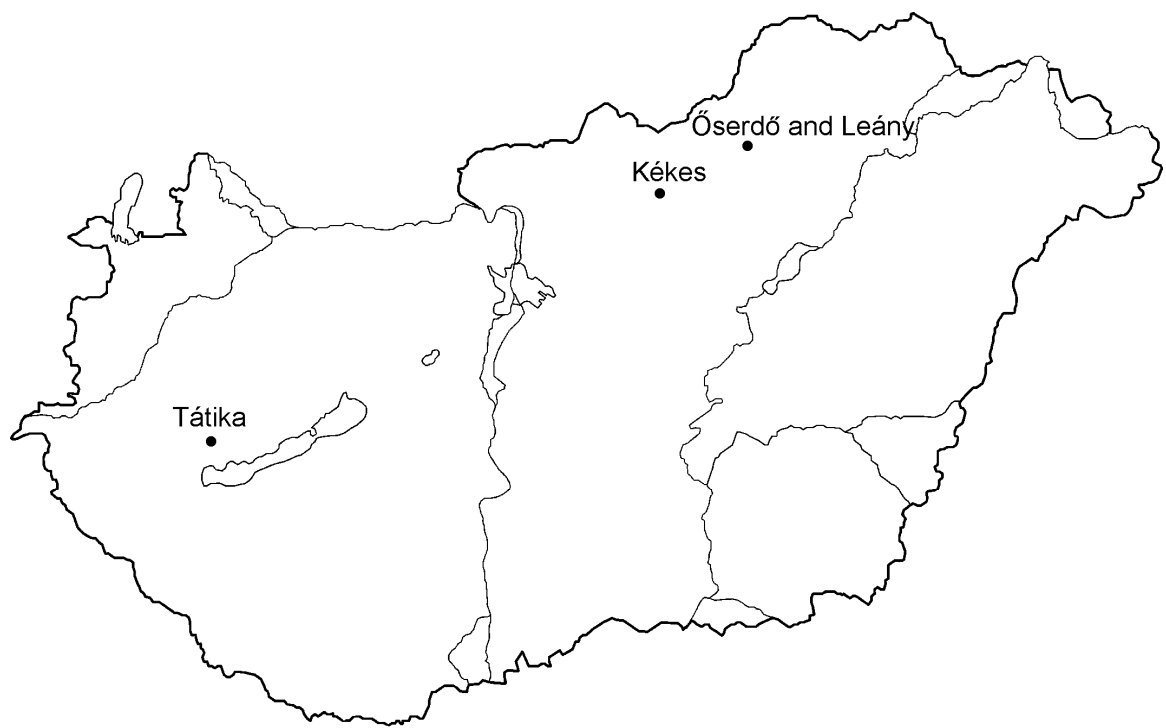


Figure 1. Location of study sites in Hungary.

Decay phases	Bark	Twigs and branches	Softness	Surface	Shape
1	intact or missing only in small patches, more than 50%	present	hard or knife penetrate 1-2 mm	covered by bark, outline intact	circle
2	missing or less than 50%	only branches (>3 cm) present	hard or knife penetrate less than 1 cm	smooth, outline intact	circle
3	missing	missing	begin to be soft, knife penetrate 1-5 cm	smooth or crevices present, outline intact	circle
4	missing	missing	soft, knife penetrate more than 5 cm	large crevices, small pieces missing, outline intact	circle or elliptic
5	missing	missing	soft, knife penetrate more than 5 cm	large pieces missing, outline partly deformed	flat elliptic
6	missing	missing	soft, partly reduced to mould, only core of wood	outline hard to define	flat elliptic covered by soil

Table 1. Classification system of decay phases.

	Tátika	Óserdő	Kékes	Leány	All sites
No. of logs sampled	111	763	111	187	1143
No. of logs with bryophytes (%)	70 (63%)	363 (49%)	108 (97%)	140 (75%)	681 (60%)
No. of species per site	31	39	36	51	75
Average no. of species per log \pm confidence limit of 95%	2.86 \pm 0.65	2.04 \pm 0.21	6.15 \pm 0.74	4.06 \pm 0.60	2.93 \pm 0.21

Table 2. General descriptors of bryophyte richness at different sites.

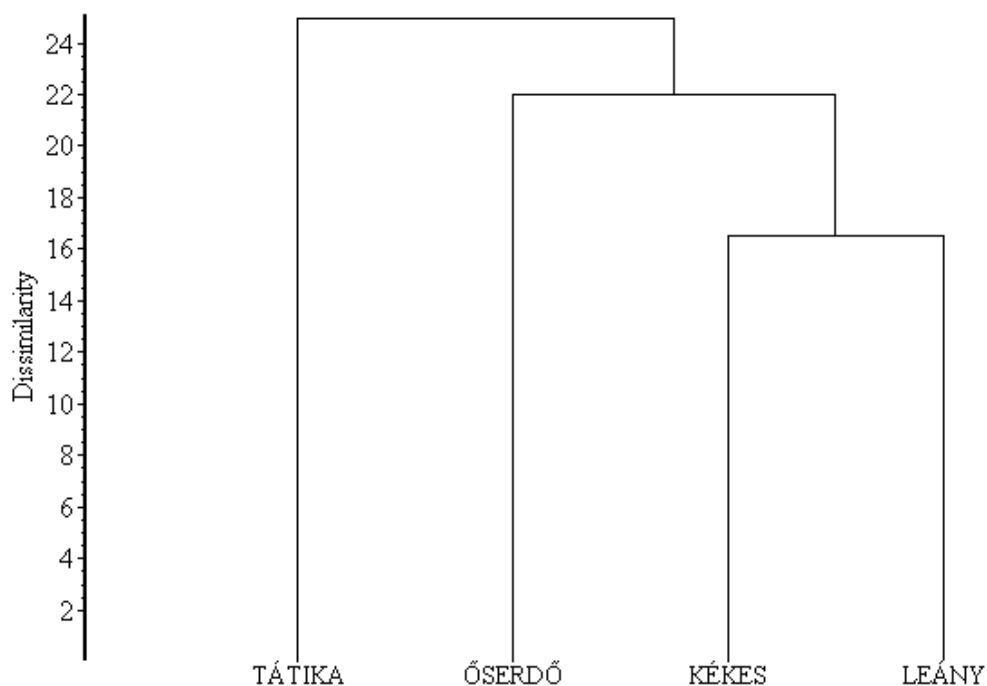


Figure 2. Agglomerative classification of sites, based on the relative frequencies of species.

SPECIES	CODE	TÁTIKA	OSERDO	KÉKES	LEÁNY	ALL	SITE	DECAY	BLOCK
Hypnum cupressiforme Hedw.	HYPCUP	15.5	12.0	14.6	9.0	12.1	***	indifferent	
Brachythecium velutinum (Hedw.) B., S & G.	BRAVEL	7.3	16.3	4.1	4.0	9.8	***	indifferent	
Amblystegium serpens (Hedw.) Br. Eur.	AMBSER	9.5	13.1	3.5	5.6	8.9	N.S.	epixyl	block1:
Brachythecium rutabulum (Hedw.) B., S. & G.	BRARUT	11.0	4.8	5.3	9.6	6.7	***	epixyl	occur all
Brachythecium salebrosum (Web. & Mohr.) B., S. & G.	BRASAL	7.6	8.9	2.2	2.0	5.7	***	epixyl	
Pseudoleskeella nervosa (Brid.) Nyh.	PSENER	6.0	2.7	2.6	1.7	2.9	*	N.S.	
Ortotrichum stramineum Hornsch. ex Brid.	ORTSTR	1.3	0.9	0.4	0.1	0.7	*	N.S.	
Platygyrium repens (Brid.) B., S. & G.	PLAREP	6.3	1.5	0.1	0.5	1.4	***	indifferent	
Amblystegium riparium (Hedw.) Br. Eur.	AMBRIPI	9.5	0.1	0.0	0.0	0.9	***	epixyl	
Homalothecium sericeum (Hedw.) B., S. & G.	HOMSER	2.2	0.5	0.3	0.6	0.7	N.S.	epiphyton	
Leucodon sciuroides (Hedw.) Schwaegr.	LEUSCI	3.2	0.4	0.4	0.4	0.7	***	epiphyton	
Frullania dilatata (L.) Dum.	FRUDIL	3.2	0.0	0.3	0.4	0.4	***	epiphyton	
Pylaisia polyantha (Hedw.) Schimp.	PYLPOL	2.5	0.2	0.0	0.4	0.4	-	-	block2:
Porella platyphylla (L.) Pfeiff.	PORPLA	2.5	0.0	0.0	0.4	0.3	-	-	occur ma
Anomodon attenuatus (Hedw.) Hüb.	ANOATT	0.6	0.2	0.0	0.2	0.2	-	-	in TÁTIK
Ortotrichum spp.	ORTSP	1.3	0.2	0.0	0.0	0.2	-	-	
Radula complanata (L.) Dum.	RADCOM	0.6	0.2	0.0	0.2	0.2	-	-	
Amblystegium varium (Hedw.) Lindb.	AMBVAR	1.6	0.0	0.0	0.0	0.1	-	-	
Homalia besseri Lob.	HOMBES	0.6	0.1	0.0	0.2	0.1	-	-	
Brachythecium populeum (Hedw.) B., S. & G.	BRAPOP	0.3	0.1	0.0	0.0	0.1	-	-	
Lophocolea heterophylla (Schrad.) Dum.	LOPHET	1.3	14.8	13.8	11.0	12.3	***	epixyl	
Bryum subelegans Kindb.	BRYSUB	1.9	5.4	4.4	3.5	4.4	***	indifferent	
Herzogiella seligeri (Brid.) Iwats.	HERSEL	0.0	4.3	6.9	2.7	4.0	***	epixyl	block3
Pterigynandrum filiforme Hedw.	PTEFIL	0.6	3.4	1.5	0.2	1.9	***	N.S.	missing c
Paraleucobryum longifolium (Hedw.) Loeske	PARLON	0.0	0.4	0.4	0.0	0.3	-	-	in TÁTIK
Dicranum montanum Hedw.	DICMON	0.0	0.2	0.0	0.0	0.1	-	-	
Pohlia nutans (Hedw.) Lindb.	POHNU	0.0	0.1	0.0	0.1	0.1	-	-	
Rhizomnium punctatum (Hedw.) Kop.	RHIPUN	0.0	3.1	6.6	8.7	4.9	***	epixyl	
Plagiomnium cuspidatum (Hedw.) T. Kop.	PLACUS	1.3	3.5	1.8	7.1	3.8	***	epixyl	
Sanionia uncinata (Hedw.) Loeske	SAIUNC	0.0	0.2	5.3	9.9	3.7	***	epixyl	block4:
Lophocolea minor Nees	LOPMIN	0.0	0.2	1.5	1.5	0.8	***	epixyl	occur ma
Metzgeria furcata (L.) Dum.	METFUR	0.0	0.5	0.7	1.1	0.6	***	N.S.	in KÉKE
Nowellia curvifolia (Dicks.) Mitt. in Godman	NOWCUR	0.0	0.0	1.6	1.1	0.6	***	epixyl	
Anomodon viticulosus (Hedw.) Hook. & Tayl.	ANOVIT	0.6	0.0	0.0	0.1	0.1	-	-	
Ceratodon purpureus (Hedw.) Brid.	CERPUR	0.0	0.1	0.1	0.1	0.1	-	-	
Dicranum scoparium Hedw.	DICSCO	0.0	0.1	9.4	0.5	2.1	***	indifferent	
Plagiothecium spp.	PLATCH	0.0	0.9	5.1	0.7	1.6	***	epixyl	block5:
Plagiochila porelloides (Torrey ex Nees) Lindenb.	PLAPOR	0.0	0.0	2.8	0.7	0.7	***	epixyl	occur ma
Isothecium alopecuroides (Dubois) Isov.	ISOALO	0.0	0.0	2.0	0.2	0.5	***	indifferent	in KÉKE
Lophozia ascendens (Warmst.) Schust.	LOPASC	0.0	0.0	0.6	0.1	0.1	-	-	
Barbilophozia barbata (Schmid ex Schreb.) Loeske	BARBAR	0.0	0.0	0.3	0.0	0.1	-	-	
Plagiomnium rostratum (Schrad.) T. Kop.	PLAROS	0.0	0.0	0.1	2.8	0.7	***	N.S.	
Blepharostoma trichophyllum (L.) Dum.	BLETRI	0.0	0.0	0.4	2.4	0.7	***	epixyl	
Riccardia palmata (Hedw.) Carruth.	RICPAL	0.0	0.0	0.0	2.5	0.6	***	epixyl	
Chiloscyphus pallescens (Ehrh. Ex Hoffm.) Dum.	CHYPAL	0.0	0.0	0.0	2.2	0.6	***	epixyl	
Mnium stellare Hedw.	MNISTE	0.0	0.0	0.0	1.2	0.3	-	-	
Cephalozia rubella var. sullivanii (Aust.) K. Müll.	CEPRUB	0.0	0.0	0.0	0.9	0.2	-	-	block6:
Eurhynchium angustirete (Broth.) T. Kop.	EURANG	0.0	0.0	0.0	0.8	0.2	-	-	occur ma
Eurhynchium hians (Hedw.) Sande Lac.	EURHIA	0.0	0.0	0.0	0.7	0.2	-	-	in LEÁN
Tortella tortuosa (Hedw.) Limpr.	TORTOR	0.0	0.2	0.0	0.2	0.1	-	-	

Table 3. Relative frequencies of species (%) at different sites and in the whole data set (“ALL”). The species are grouped by block clustering. SITE gives the significance level for the factor "site" (*: $p < 0.05$, ***: $p < 0.001$, N.S.: non-significant). DECAY gives the classification based on the interpretation of the logistic regression analysis.

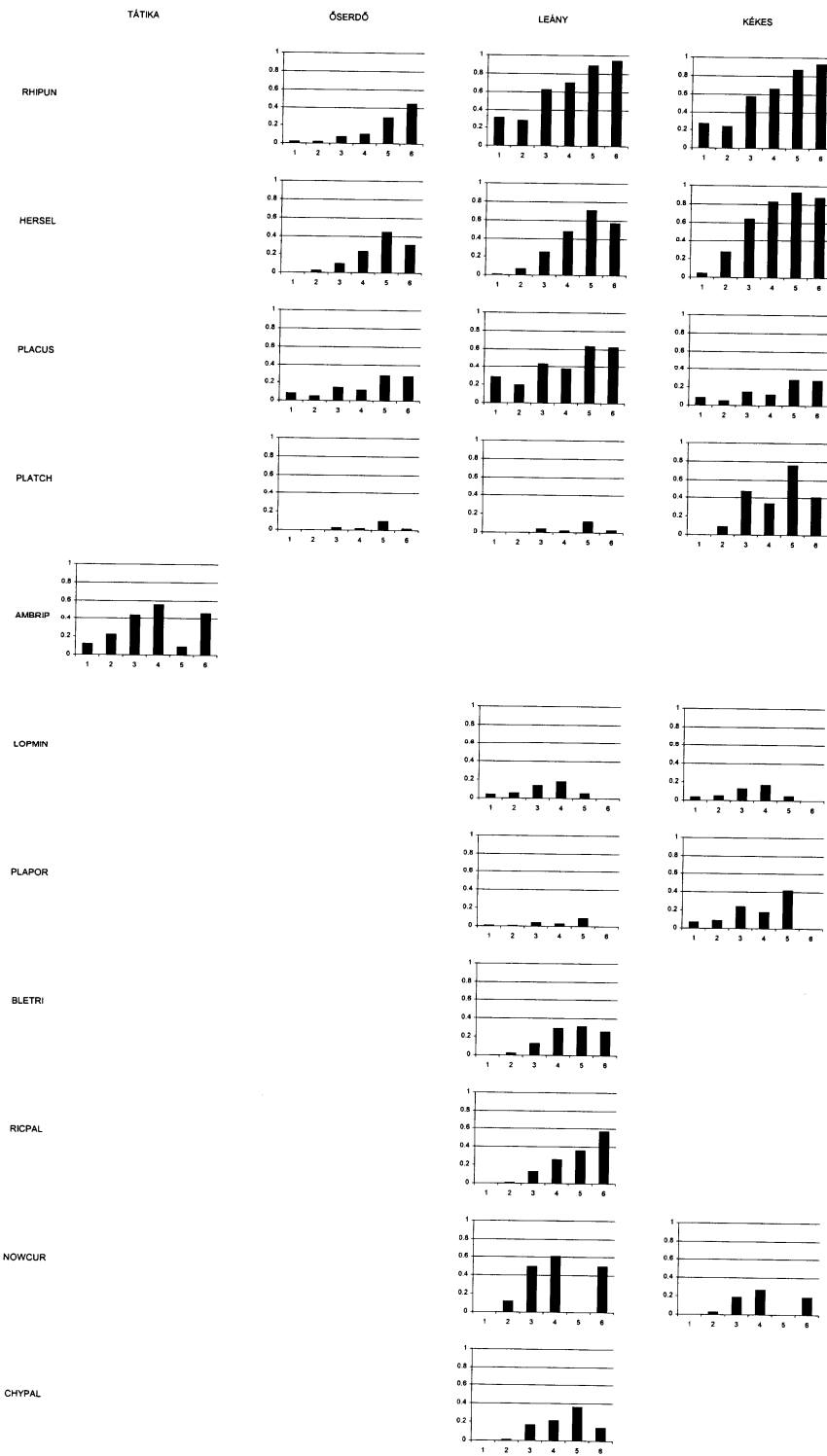


Figure 3. Predicted effect of decay phase on the occurrence of epixylic species based on logistic regression analysis with a log volume of 0.5 m^3 . X axis: decay phase categories; Y axis: occurrence probability. Full names of the species are given in Table 3.

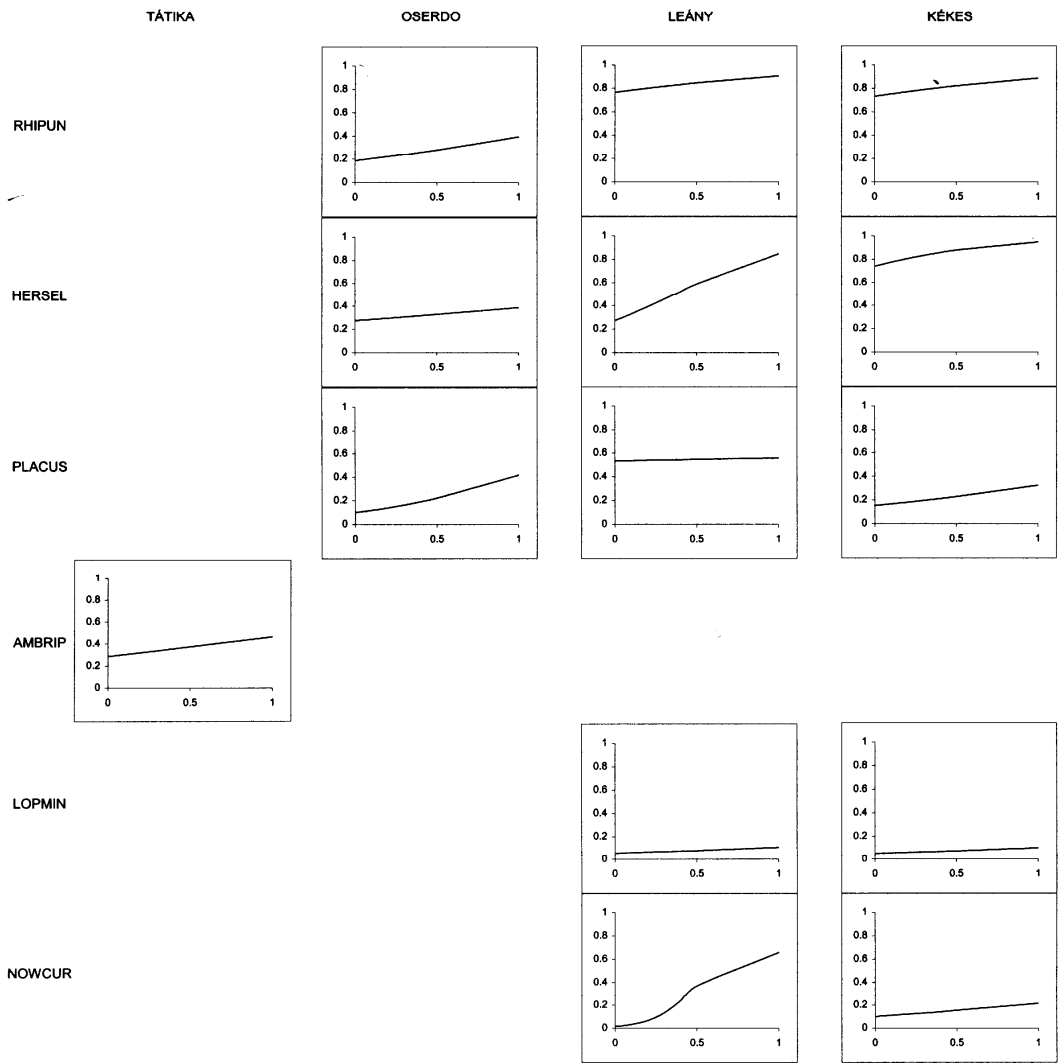


Figure 4. Predicted effect of volume on the occurrence of epoxylic species based on logistic regression analysis, predictions are averages for decay phases 4 to 6. X axis: volume in m³; Y axis: occurrence probability. Full names of the species are given in Table 3.

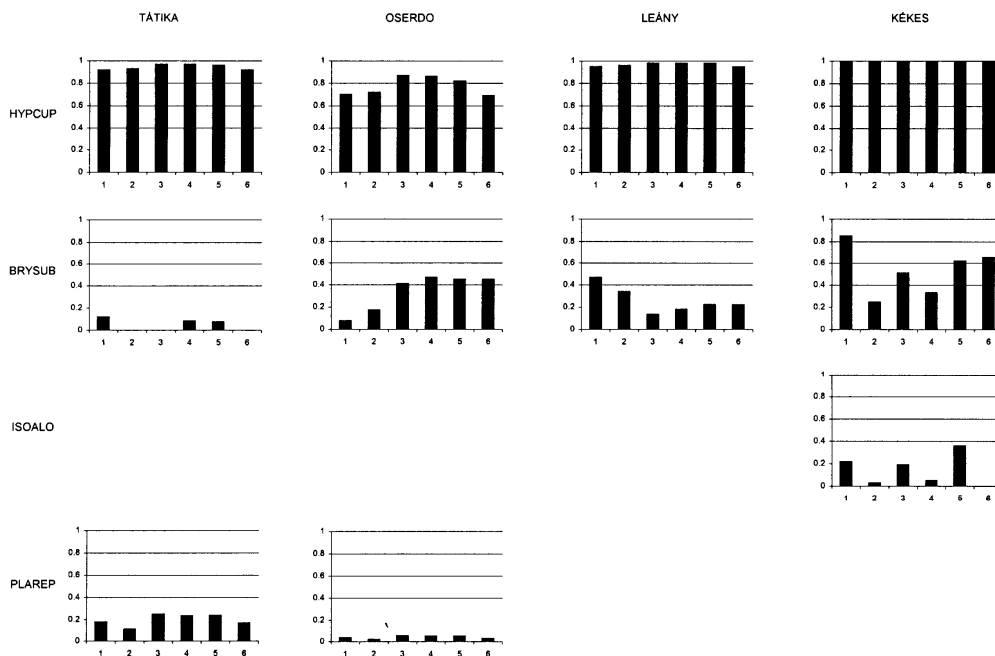


Figure 5. Predicted effect of decay phase on the occurrence of indifferent species based on logistic regression analysis with a log volume of 0.5 m³. X axis: decay phase categories; Y axis: occurrence probability. Full names of the species are given in Table 3.

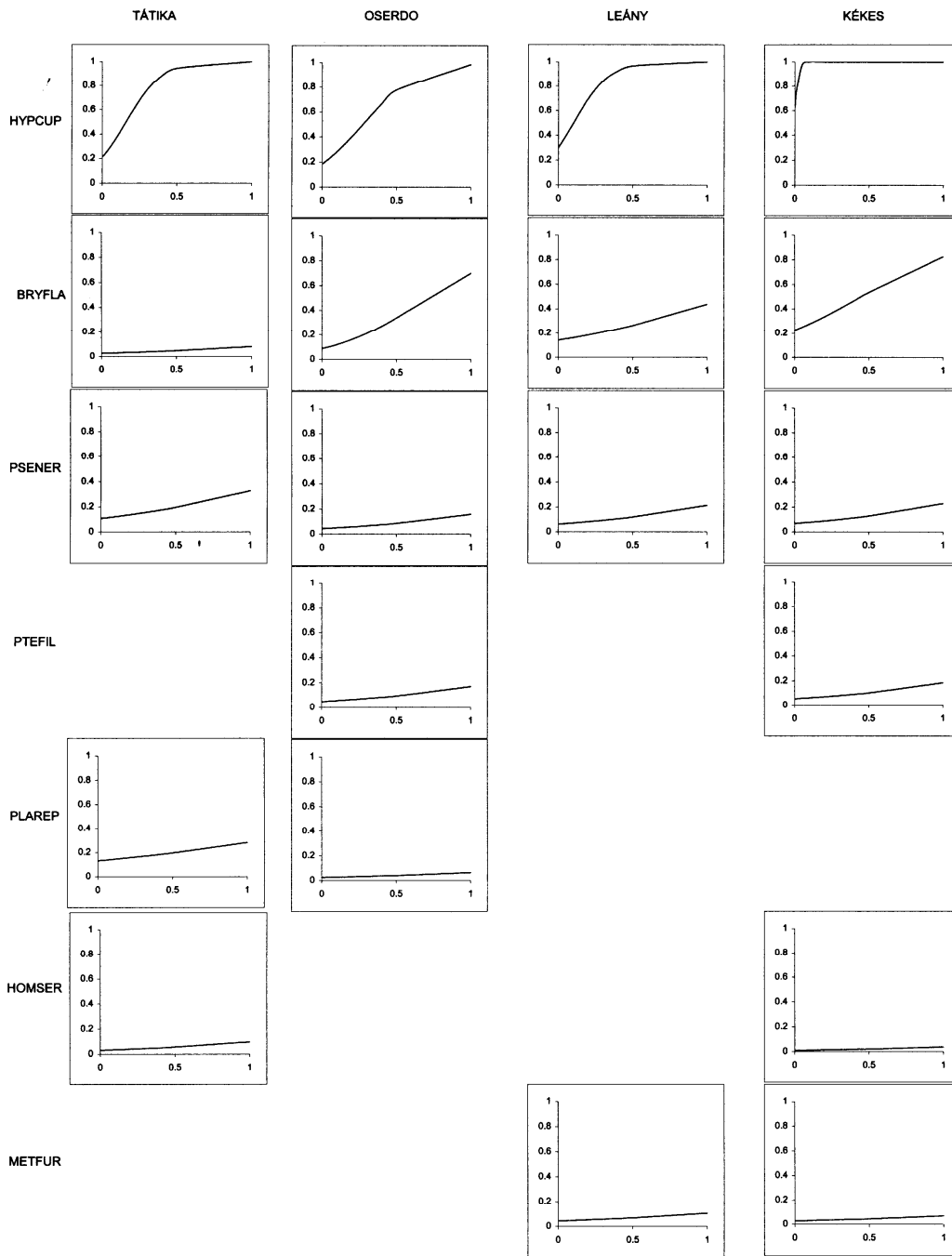


Figure 6. Predicted effect of volume on the occurrence of indifferent species based on logistic regression analysis, predictions are averages for decay phases 1 to 6. X axis: volume in m³; Y axis: occurrence probability. Full names of the species are given in Table 3.

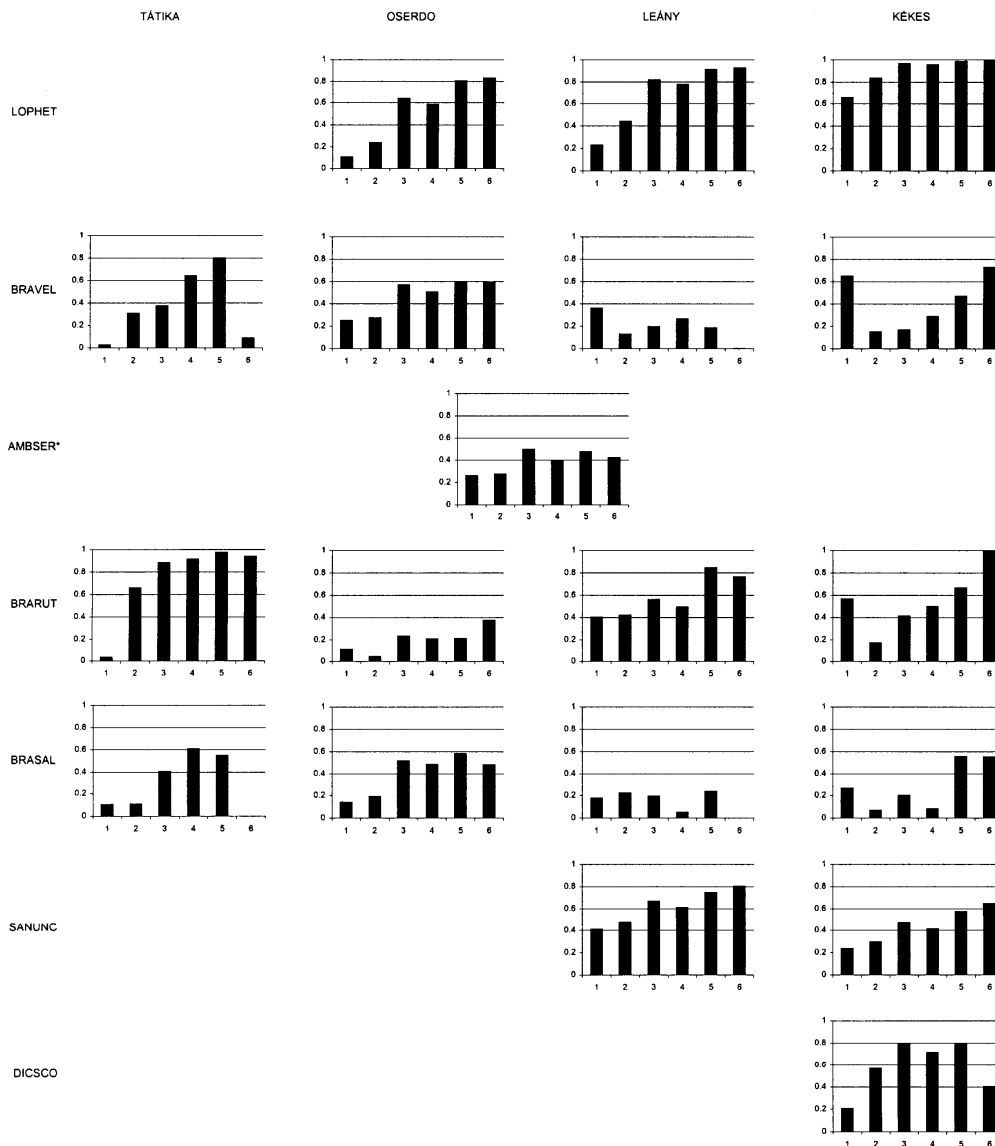


Figure 7. Predicted effect of decay phase on the occurrence of epixylic species with a wide tolerance based on logistic regression analysis with a log volume of 0.5 m^3 . X axis: decay phase categories; Y axis: occurrence probability; *: the factor "site" is not significant. Full names of the species are given in Table 3.

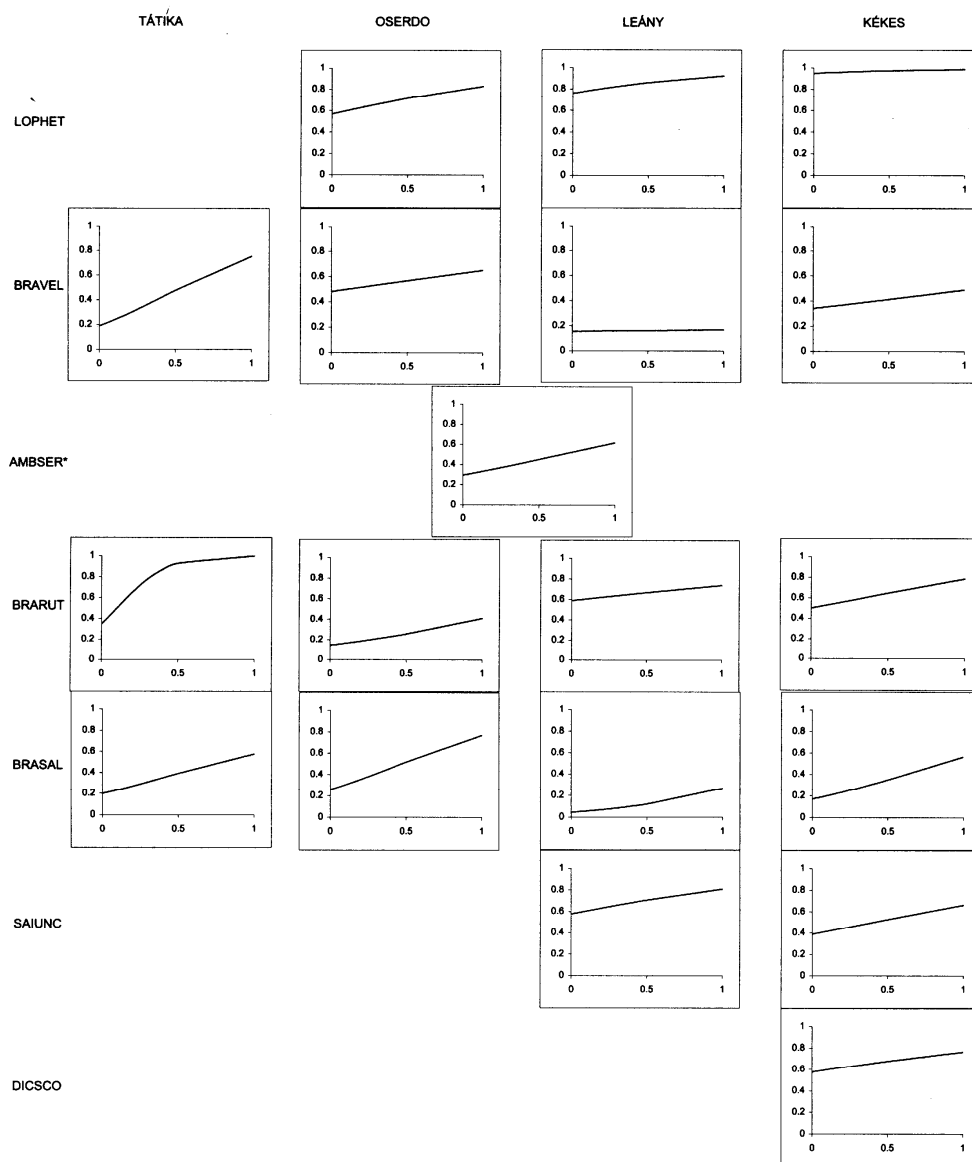


Figure 8. Predicted effect of volume on the occurrence of epixylic species with a wide tolerance based on logistic regression analysis, predictions are averages for decay phases 3 to 6. X axis: volume in m^3 ; Y axis: occurrence probability; *: the factor "site" is not significant. Full names of the species are given in Table 3.

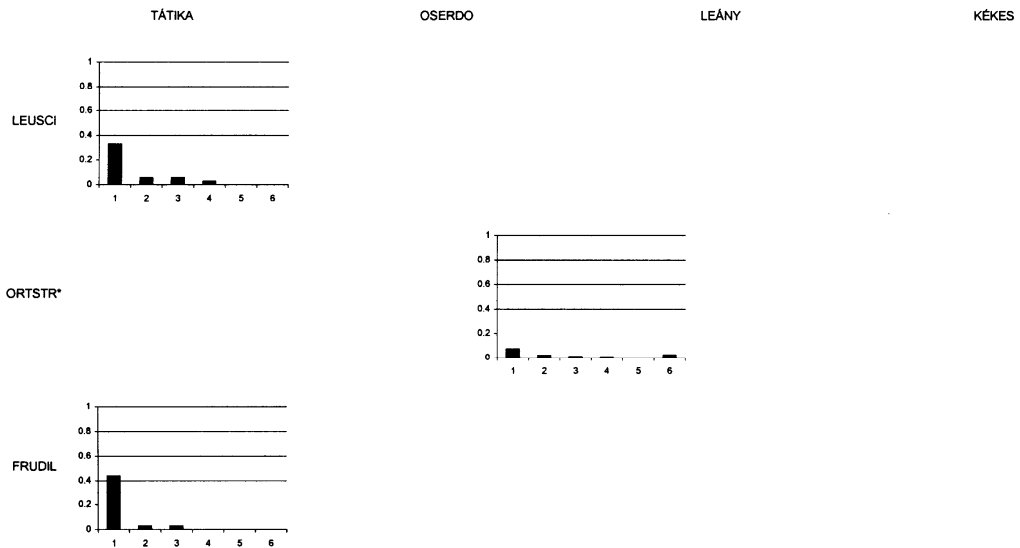


Figure 9. Predicted effect of decay phase on the occurrence of epiphyte species based on logistic regression analysis with a log volume of 0.5 m^3 . X axis: decay phase categories; Y axis: occurrence probability; *: the factor "site" is not significant. Full names of the species are given in Table 3.

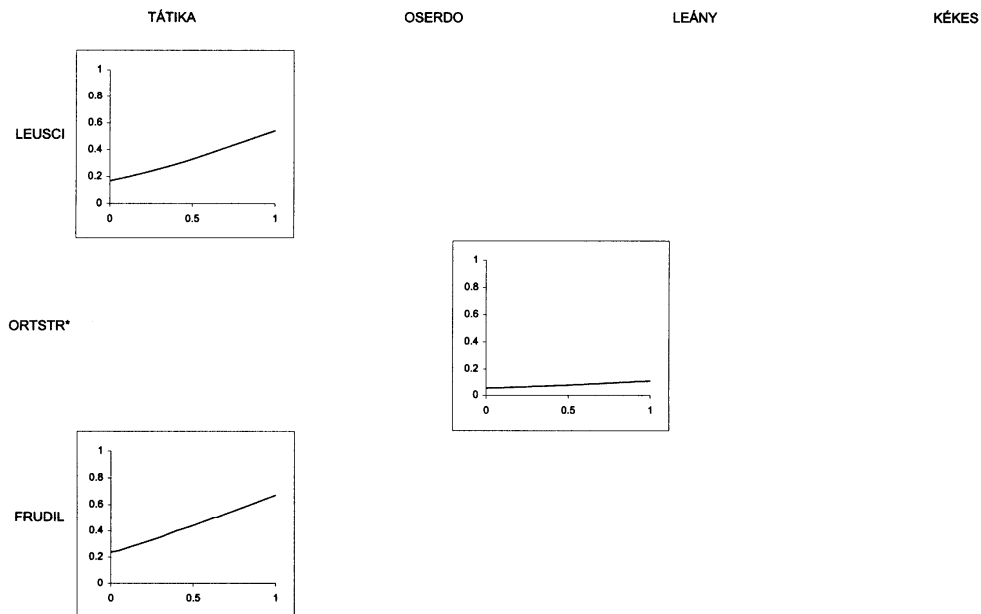


Figure 10. Predicted effect of volume on the occurrence of epiphyte species based on logistic regression analysis, predictions are restricted to decay phase 1. X axis: volume in m^3 ; Y axis: occurrence probability; *: the factor "site" is not significant. Full names of the species are given in Table 3.

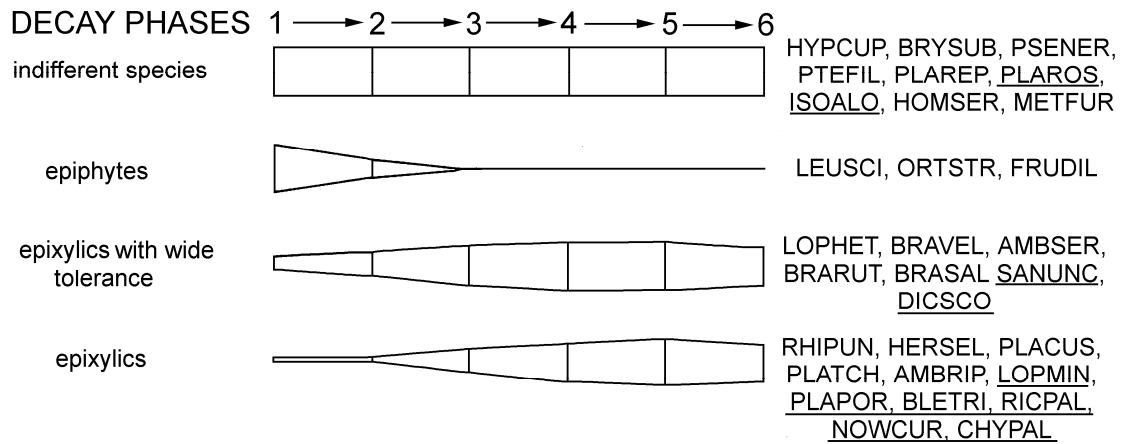


Figure 11. Generalised distribution of different species groups (indifferent species, epiphytes, wide tolerant epixylics, epixylics) along decay phases. The width of band represents the relative frequency of species at different decay phases. Underlined species are limited to ravine-like forests. The effect of log size is excluded from this successional scheme. Full names of the species are given in Table 3.