The importance of coarse woody debris for bryophyte vegetation of semi-natural beech forests

PhD Thesis

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"...S majd este lesz, és rámkövül sarával
az éjszaka, s én húnyt pillák alatt
őrzöm tovább e vonulást, e lázas
fácskákat s ágacskáikat.
Levelenként a forró, kicsi erdőt.
Valamikor a paradicsom állt itt.
Félálomban újuló fájdalom:
hallani óriási fáit..."
Pilinszky János: Apokrif

"...Evening will come, and night will petrify
above me with its mud. Beneath closed eyelids
I do not cease to guard this procession
these fevered shrubs, their tiny twigs.
Leaf by leaf, the glowing little wood.
Once Paradise stood here.
In half-sleep, the renewal of pain:
to hear its gigantic trees..."
János Pilinszky: Apocrypha
[Ted Hughes & János Csokits]

Table of contents

List of Papers included in the thesis

I. Ódor, P. 2000. Description of the bryoflora and bryophyte vegetation of Kékes North Forest Reserve in Mátra mountains (N-Hungary). Kitaibelia 5(1): 115-123. (in Hungarian).

II. Ódor, P. and Standovár, T. 2002. Substrate specificity and community structure of bryophyte vegetation in a near-natural montane beech forest. Community Ecology 3(1): 39-49.

III. Ódor, P. and Standovár, T. 2001. Richness of bryophyte vegetation in a near-natural and managed beech stands: The effects of management-induced differences in dead wood. Ecological Bulletins 49: 219-229.

IV. Standovár, T., Ódor, P. Aszalós, R. and László Gálhidy. Spatial diversity of ground layer vegetation as a sensitive indicator of forest naturalness. Submitted manuscript.

V. Ódor, P. and van Hees, A.F.M. Preferences of dead wood inhabiting bryophytes to decay phase, log size and habitat types in Hungarian beech forests. Accepted manuscript, Journal of Bryology.

Introduction

This thesis consists of five studies on the bryophyte vegetation of semi-natural beech forests and the effects of coarse woody debris (CWD) on it. Although these papers are independent publications, they are closely related to each other, representing different stages of a uniform investigation. The order of the papers represents a temporal progress of the investigation. In Papers I-II, the scientific questions are more general and the results give elementary information about the bryophyte vegetation of semi-natural beech forests. Papers III-IV compare the bryophyte and vascular vegetation as well as the amount of dead wood in semi-natural and managed beech stands. The last paper (Paper V) focuses on the questions of succession and diversity of log inhabiting bryophyte vegetation in different semi-natural beech stands.

Importance of CWD in temperate forests

A major feature of unmanaged old-growth forests in temperate region is the high amount of dead wood (Peterken 1996), which appears as standing dead trees (snags), fallen dead trees (fallen logs and branches), stumps, dead limbs on living trees, decay columns in trunks and rot holes in standing trees (Ferris-Kaan et al. 1993, Csóka 2000). Based on size, dead wood is divided into fine woody debris (FWD) and CWD, although the diameter limit of these categories differs considerably in the literature: 10 cm in Kruys and Jonsson (1999), 2.5 cm in Harmon et al. (1986) and Peterken (1986). From biological pont of view it makes sense to categorise dead woody material as litter if its diameter is less than 5 cm, as FWD between 5 and 10 cm and as CWD above 10 cm according to Kruys and Jonsson (1999). Most of the studies estimating the amount of dead wood include logs thicker than 10 cm.
Concerning near-natural stands, the amount of CWD can considerably differ among forest types in the temperate region. It can depend on the disturbance regime and productivity of the habitat (Petereken 1986, Runkle 1985, Harmon et al. 1986, Siitonen 2001), which influence the CWD input, and on the tree species and environmental conditions determining the rate of decay. Generally, the amount of CWD is higher in coniferous than in broad-leaved forests, because coniferous trees decay slower due to their higher extract material and lignin content (Harmon et al. 1986). In old-growth stands the average volume of CWD varies from cca. 90 to 120

m^3/ha in Fennoscandian mesic spruce forests (Siitonen 2001), cca. 60 to 120 m^3/ha in pine forests (Siitonen 2001), cca. 400 to 1400 m^3/ha in North-American Pseudotsuga-Tsuga forests, 50-130 m^3/ha in North-American deciduous forests (Harmon et al. 1986), cca. 40-70 m^3/ha in British deciduous forests (Kirby et al. 1997), cca. 150-280 m^3/ha in Dynaric beech-fir forests (Hartman 1999), and cca. 80-130 m^3/ha in Hungarian beech forests (Ódor Paper V). The distribution of CWD in space and time could considerably vary depending on the disturbance regime of the habitat. In forest types where the major disturbance agents take effect at a coarse spatial scale (fire, windstorms), the distribution is relatively even at large spatial scale (the scale of disturbance), but varies considerably in time. The amount of CWD depends on the time elapsed since the last disturbance (Harmon 1986, Siitonen 2001, Runkle 1985, Esseen et al. 1997). In forests, where fine scale gap formation is characteristic (permanent uneven-aged stand structure), the presence of CWD in different stages of decay is continuous. In this case the spatial distribution of CWD is aggregated at a finer scale following the scale of disturbances and the "shifting mosaic" structure of the forest (Watt 1947, Runkle 1985, Peterken 1986, Korpel 1995, Emborg et al. 2000).

Because of timber production and forest management, the quantity of CWD drastically decreased in forests and forest remnants. In near-natural, old-growth forests the amount of dead wood is much higher than in managed forests: cca. 10-15 times in boreal region (Jonsson, 2000, Andersson and Hytteborn, 1991, Lesica et al., 1991, Samuelsson et al. 1994) and cca. 4-5 times in broad-leaved forests (Ódor and Standovár Paper III, Green and Peterken, 1997, Kirby et al. 1997). Unmanaged and managed forests also differ considerably in the quality of dead wood (Söderström, 1988a, Jonsson, 2000, Kruys et al., 1999, Ódor and Standovár, 2001, Andersson and Hytteborn, 1991, Rambo and 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. In managed stands, even though, the proportion of fine woody debris (small branches and logs) and stumps is high, well-decayed logs are underrepresented and the presence of dead wood depends mainly on forestry activities (Kruys et al. 1999, Christensen and Emborg 1996, Csóka 2000).

The major parts of tree trunks are outer bark, inner bark, sapwood and heartwood (Maser and Trappe 1984). The inner bark and the sapwood have the highest nutrient

content, these are the first colonisation places of insects and fungi, and their decay is fast. The outer bark and the heartwood have a high lignin and extract material content and they resist decay relatively long. The time of decay depends considerably on log diameter, because in the case of large logs the proportion of heartwood is higher and more time is needed for the colonisation of decomposers. During decomposition, physical, chemical and also biological processes can be observed. These are leaching, fragmentation, respiration of wood living organisms and biological transformation. In the two latter processes, the role of fungi is considerable. In the final decay stages cca. 35% of the biomass of trees is fungi biomass, mainly chitin (Harmon et al. 1986). The species composition of fungi basically determines the decay processes. During decay the first colonisers are heartrot fungi (they occur in living trees by latent propagules), pathogens and R-selective pioneers (colonising at wounds and in fissures) (Boddy 2001). Later, different Basidiomycetes appear with higher competitive ability. They colonise from fissures and replace the pioneers. There are some rhizomorph and cord forming species among them. It is important to distinguish physiologically between white rot fungi (decomposing both lignin and cellulose) and brown rot fungi (decomposing only cellulose and hemicellulose). The mycelia of different species are usually separated in trunks, forming decay columns. The succession of fungi considerably depends on tree species, environmental and historical factors, and - mainly in the case of latest decay stages- stochastic events (Heilmann-Clausen 2001, Boddy 2001). Decay processes on snags and logs are different. As decay proceeds the log loses its bark, the woody material gets soft, it loses its structure, the log becomes flat and sinks slowly into the ground. Individual decay processes can deviate from this rough general scheme: sometimes the outer bark remains on the log for a longer period or the well-decayed woody material retains its hardness due to the presence of some fungi (e.g. some *Pyrenomycetes* species). In wet habitats decay could be very different: here bacteria are more important agents of decay than fungi and the exploiting invertebrates are also different (Harmon et al. 1986, Maser and Trappe 1984). Based on the outer characteristics of decay (bark cover, softness of wood, structure of wood surface, shape of bole etc.), the decay stage of dead trees was classified into decay phases (Fehér and Orbán 1981, McCullogh 1948, Raschendorfer 1949, Muhla and Leblanc 1975, Sippola and Renvall 1999, Maser and Trappe 1984, Söderström 1988b, Paper III, Paper V). These systems are considerably different, having 3 to 8 categories and the most important features of type definitions also vary.

There are some classification schemes that, apart from the outer characteristics of dead trees, take vegetation characteristics (e.g. moss cover, presence of seedlings) (see in Söderström 1988b) or nutrient content into account. We cannot expect to have a common scheme for classifying decay types which is valid for a large region, because features of decay could be very different depending on tree species and environmental conditions. Characterising decay using decay types could be more appropriate biologically than the duration of decay: although these systems are accused of subjectivity, the duration of decay considerably depends on log size (a thin log can reach the same decay stage much faster than a large one).

Dead wood plays an important role in nutrient cycling and geomorphologic processes in forests (Harmon et al. 1986, Krankina et al. 2002), building a long term nutrient storage and preventing erosion processes. Maybe the most important feature of dead wood is that thousands of species (e.g. fungi, bryophytes, lichens, invertebrates, amphibians, cavity nesting birds, bats, small mammals) need dead wood as living, breeding and nesting site. The survival of these populations may depend on the quantity and quality of dead wood. In boreal forests tree regeneration is facilitated by nurse logs (Samuelsson et al. 1994; Harmon et al. 1986; Esseen et al. 1997; Hofgaard 1993). CWD could be an important habitat for forest herbs both in flood-plain forests (Dennis and Batson 1974) and in other temperate forest types (Thompson 1980, Schaetzl et al. 1989). The importance of dead wood for different organisms has been reviewed in different parts of the 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 and Ziegler, 1991, Siitonen 2001). A lot of saproxyl fungi are missing from managed forests because of the lack of dead wood (Siller 1986, Sippola and Renvall 1999). There are many invertebrate species that depend obligatorily on dead wood. There are only rough estimations concerning their number, but it is cca. 3500 in European boreal forests (Siitonen 2001) and based on the estimation of Csóka (2000) it could be higher in the broad-leaved zone due to higher tree diversity. There are excellent reviews concerning the temperate region, which describe the most important invertebrate groups relying on dead wood (Harmon et al., 1986; Maser and Trappe, 1984; Esseen et al., 1997; Samuelsson et al., 1994, Siitonen 2001). The effects of invertebrates are also very important in decomposition processes. In early decay stages their channels are good sites for fungi colonisation (e.g. bark beetle channels) and in later stages they are important mixing and decomposing agents (e.g.

Collembolans, earthworms). Among vertebrates dependent on dead wood (many amphibians, birds, bats, small mammals) woodpeckers are a key-species group, because a lot of cavity nesting birds, bats and small mammals use their cavities. The number and diversity of woodpeckers considerably determine the diversity of other organisms (Sandström 1992, Csóka 2000, Mikusinski and Angelstam 1997).

The effect of CWD on bryophyte vegetation

Plenty of bryophyte species occur on dead wood obligatorily (true epixylics) or facultatively (epiphytes, epigeic and epilithic species). For example, 11% of the Hungarian bryoflora (62 species) occur mainly on dead wood (based on Orbán and Vajda 1985), and in a small region in Romania (Ariesului mic basin) 106 species were described from this substrate (Goia and Schumacher 2000). In an investigation of the bryophytes on dead wood in four Hungarian semi-natural forests, 75 species occurred on this substrate (Paper V). On 200 beech logs in two old-growth beech-fir forests in Slovenia, 102 log inhabiting species were found (Ódor and van Dort, unpublished data). Because the availability and continuity of this substrate dramatically decreased in managed landscape (Söderström and Jonsson 1992, Söderström 1989, Söderström 1990), several obligate epixylic species with narrow habitat requirements and limited dispersal ability have become threatened in Europe (ECCB 1995). Numerous studies from different regions compare the diversity of bryophyte vegetation of unmanaged and managed stands (Lesica et al. 1991, Gustafsson and Hallingbäck 1988, Andersson and Hytteborn 1991, Söderström 1988, Rambo and Muir 1998, Paper III, Paper IV). In boreal forests the differences between semi-natural and managed stands are less pronounced in species richness of stands and diversity indices. On the other hand, the species richness on logs is much higher in natural stands and the compositional differences are considerable (Lesica et al. 1991, Gustafsson and Hallingbäck 1988, Anderrson and Hytteborn 1991). In Hungarian beech forests natural stands differ from managed ones mainly in the number of epixylic species, in the more even frequency distribution of species, and in their more fine-grained spatial pattern (Paper III, Paper IV). The high amount of dead wood could also increase the diversity of rupicolous bryophyte communites (Paper II). A common conclusion of these comparative studies is that a group of obligate epixylics (mainly liverworts) can survive only in near-natural forest remnants, because they need a continuous presence of large logs in

medium and late decay stages, and a constantly high level of air humidity. These characteristics are usually missing from managed stands.

Although the importance of dead wood for bryophytes is clear, the description of the species' preferences to dead wood features, their succession on logs and the determination of dead wood dependent assemblages are not always obvious. At large geographical scale the potential bryophyte vegetation on logs (the species pool) is closely related to the major vegetation (and climatic) types. For example in British Columbia, most of the epixylic species have a narrow distributional range and are connected to one biogeoclimatic zone (Qian et al. 1999). In Europe, the major difference among communities is also their connection to vegetation zones according to the described epixylic bryophyte associations (Barkmann 1958, Phillippi 1965, Hübschmann 1986, Marstaller 1987). From regional studies, it is evident that moisture conditions (mainly air humidity) are the most important factor determining species composition of forests rich in dead wood. In more humid forests the species richness and the abundance of hepatic species are 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). Investigating different forest types in North Carolina, McAlister (1997) found that the most important factor influencing species composition is the phorophyte type (conifer or broad-leaved). Although the climatic and regional edaphic differences can modify considerably the way of succession, all investigations concentrating on one habitat type reveal a clear compositional change during decay. This statement is independent of the fact that the theoretical background of studies has a phytosociological (Muhle and Leblanc 1975, Cornelissen and Karssemeier 1987, Fehér and Orbán 1981) or an individualistic point of view (Söderström 1988, Rambo and Muir 1998, McCullough 1948, Kruys et al. 1999). In the temperate broad-leaved region most bryological studies on dead wood follow the synusial concept of vegetation science (Barkmann 1973), whose major task is to describe and hierarchically classify the bryophyte associations. The number of epixylic associations is very high (in addition, epiphytic and terricolous associations can also occur on dead wood), and their system is quite complicated (Barkman, 1958; Hübschmann, 1986; Marstaller, 1986). It is very instructive to compare the system made independently by Hübschmann (1986) and Marstaller (1986) about epixylic associations. Although the described associations differ in their characteristic species

(which are sometimes very rare), their species composition considerably overlaps. Although the authors describe the habitat preferences of associations, in these descriptions the factors considering geographical (climate, vegetation zones), edaphic (local air humidity, soil conditions, bedrock), naturalness (stand age, stand continuity, amount and distribution of dead wood) and tree level (decay, size, stump-snag-log) features are mixed. 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 into four categories, which reflect their preference to different decay phases: epiphyton-corticol, epixylic, sapro-lignicol and humicol-terricol species (sensu Stefureac, 1969) or epiphytic, early epixylic, late epixylic, and ground flora species (sensu Söderström, 1988b). It is not clear if this classification can be transferred directly to broad-leaved forests as litter accumulates on the forest floor and a well-developed terrestrial bryophyte layer is missing. In the case of Central-European beech forests Ódor and van Hees (Paper V) propose a classification for dead wood inhabiting species as epiphytes, indifferent species, wide tolerant epixylics and epixylics.

Several studies have addressed the importance of log size for species composition and species richness of dead wood (Söderström 1988a, Rambo and Muir 1998, Kruys and Jonsson 1999, Kruys et al. 1999, Paper III, Paper V). Generally, epixylic species (mainly epixylic hepatics) are restricted to large logs. Small logs and branches decay fast and are easily covered by litter and are overgrown by terrestrial species. They are a suitable habitat for epixylic species only for a short period. Furthermore, a lot of epixylic species have a low dispersal capacity, which limits the probability of colonising small logs and branches (Söderström 1988b). Söderström (1989, 1990) classified epixylic liverworts based on their local and regional distribution. Locally and regionally rare species are very sensitive to fragmentation, and they need the continuous presence of CWD in their neighbourhood. Many species among saproxylic beetles and insects are also very sensitive to fragmentation. For these species, the regional spatial distribution of old-growth stands is also important besides stand level characteristics (Siitonen et al. 2001).

There are very few investigations concerning the dynamics of dead wood inhabiting bryophyte vegetation, so most of the statements about the mechanisms involved are only hypotheses. The first colonisers of CWD are bark living epiphytes. They show a

similar vertical pattern on snags as on living trees: on the bottom part epigeic species occur as facultative epiphytes, while on the drier upper part true epiphytes can be found (Smith 1982a, Barkman 1958). The majority of snags do not reach later decay stages as a snag because of disintegration. First epiphytes and indifferent species colonise the bark of logs as well (Paper V). Because the microclimatic conditions along logs are more stable than at standing trees, the bark inhabiting bryophyte cover could be much higher than on standing trees. Most of these bryophytes colonise after tree-fall, mainly in small fissures and bark holes. The cover of fast growing (usually opportunistic) pleurocarp species is higher than that of epiphytic acrocarps and liverworts. After 3-6 years, when the bark is fallen off in large patches, logs loose their original bryophyte cover rapidly and bryophytes have to colonise the hard or soft woody surfaces. True epixylic species can colonise only the soft woody material. The stability of the bryophyte cover on this substrate is lower than on the bark or the hard wood, and the mortality of shoots is faster. Usually, well-decayed logs are also dominated by pleurocarps, but the cover of liverworts could also be high. The gaps in the bryophyte layer could be overgrown by the original species or are filled by gap dependent species such as some acrocarp mosses or liverworts. Some species, e.g. *Tetraphis pellucida,* cannot germinate in the presence of pleurocarp competitors, only in open softwood gaps (Kimmerer 1991). The species composition of logs depends on the size, position and frequency of gaps (disturbance regime) (Kimmerer and Young 1996), and the species pool, dispersal limits, and the competitive relations of species. Competition between species could be important at germination (Kimmerer 1996, 1997). Studying niche width and overlap of epixylic bryophytes Söderström (1988c) concludes that dispersal and colonisation are more important for the spatial pattern of species than interspecific competition. Numerous epixylic species maintain their local populations by gemmae, which can germinate very fast in gaps (Kimmerer 1991, Laaka-Lindberg 2000). In latest decay phase epixylic species disappear. In boreal forests logs are overgrown by ground floor species, whereas in deciduous forests litter accumulation and increasing vascular cover prevent their survival and colonisation.

Short presentation of the papers

Paper I gives a qualitative description concerning the bryoflora and bryophyte vegetation of Kékes North Forest Reserve. The studied area is a semi-natural montane

beech dominated forest stand in the Mátra mountains. This is an old-growth forest without any forest management activities in the past. It is characterised by the high amount of dead wood, uneven-aged stand structure (mosaic of different forest developmental phases) and heterogeneous topographic conditions (Czájlik et al. 1993, Czájlik 1996, Gálhidy 1999, Pászty 1998). The study describes the abiotic and biotic conditions of the area and its bryophyte vegetation, and also lists the species found there. Abundance, ecological requirements and substrate specificity of the species are characterised. The importance of the reserve in biological conservation is enhanced on the basis of bryophyte vegetation. In the 64 ha core area, 20 liverwort species and 48 moss species were found. This species pool is cca. 12% of the Hungarian bryoflora (Orbán-Vajda 1983), although there are no wetlands in the reserve. Both the high environmental heterogeneity and the naturalness of the reserve contribute to this very high species richness. One liverwort is new to the Hungarian flora (*Anastrophyllum hellerianum*), and other five liverwort species to the Mátra mountains (*Calypogeia muelleriana, Calypogeia suecica, Lophozia ascendens, Lophozia longiflora, Nowellia curvifolia*). *Lophozia ascendens* is the only *Lophozia* species in Hungary which is included in the Red Data Book of European Bryophytes (ECCB 1995) as a "rare" category species. For the survival of these rare epixylic species the continuous presence of large, well-decayed logs is needed. During the decay process, the local populations of epixylic species become extinct, and they have to colonise new logs at appropriate level of decay and within limited spatial distance (Söderström 1989, Söderström and Herben 1997). Although a bryophyte vegetation rich in species can be found in the fissures of andesite outcrops in ravine like sites and on rock walls, the bryophyte vegetation occurring on decaying logs makes the reserve unique.

The statements of Paper I were based on field experience and a list of species. To describe the structure of this bryophyte vegetation, more detailed studies were needed investigating the following questions: (1) To what extent do different species prefer different substrate types (CWD or rock)? (2) Which assemblages of species are the most important? (3) To what extent do the occurrences of species differ from random combination of them?

Paper II describes the same bryophyte vegetation as Paper I, but in a more quantitative way. A 120 m by 120 m plot of the Kékes Forest Reserve was systematically sampled in 0.5 m by 0.5 m quadrats that were set out on a grid at 5 m intervals. In each of the quadrats, nine 100 cm² microplots were set out

systematically. In these microplots, presence of bryophyte species and the type of the substrate were recorded. Substrate specificity and interspecific relationships of the species were analysed based on presence/absence data of 1508 microplots. Of the species occurring with frequencies higher than 10, 8 are associated to rock, 5 to dead wood, and 5 to both substrate types. Analyses of interspecific associations and agglomerative classification reveal that frequent species of species poor bare rocks are separated from species rich assemblages of humus rich outcrops and coarse woody debris. Organic matter among rocky outcrops originates from CWD. In consequence of organic matter accumulation, there is an overlap between the species pool of humus rich outcrops and that of dead wood. This study suggests that the presence of CWD not only provides habitat for bryophytes inhabiting dead wood, but also results in diverse epilithic bryophyte assemblages on outcrops rich in humus. In reality, bryophytes living on decaying woods and outcrops are not separated as distinctly as phytosociological descriptions suggest (Philippi 1956, Barkmann 1958, Hübschmann 1986). The species composition of humus rich outcrops differs to a greater extent from that of bare rock surfaces, which are ordered to the same synusia, than from that of decaying woods. Monte Carlo simulations reveal that many species combinations are significantly more frequent than expected under the assumption of random combining of species. The observed number, diversity and evenness of species combinations are significantly lower, whereas spatial dependence (expressed as associatum) is significantly higher than under the neutral models even when data are stratified according to substrate types. Many studies show that bryophytes behave opportunistically, the effects of niche segregation are negligible, existing mats have positive feedback to establishment, and mortality is not density dependent (Slack 1977, Lee and La Roi 1979, Watson 1980, Sadler and Bradfield 2000). These could be true for assemblages of humus rich outcrops and CWD, but not for species of exposed rock surfaces, where fast growing (*Hypnum cupressiforme*) and colonist (*Grimmia hartmanii*) species can dominate, and the number of realised species combinations is limited.

Papers I and II show that the diversity of bryophyte vegetation in the investigated reserve is very high, and the role of CWD is very important. It is supposed that the bryophyte diversity of managed stands is lower than that of the reserve because of the lack (or much lower amount) of CWD.

Paper III compares the diversity of bryophytes and the quantity and quality of CWD in Kékes North Forest Reserve with five neighbouring managed stands of different ages. Species richness, abundance, different diversity measures and species composition were analysed based on 50 m by 50 m sample plots in which blocks of 100 cm² microplots were systematically distributed and presence/absence data of bryophytes were collected. In the reserve two plots were investigated representing considerably rocky and less rocky habitat types. Amount of dead wood and its distribution according to size and decay phases were estimated in each plot. The bryophyte vegetation was richer in the near-natural stand, especially in the moist rocky site. Species richness, abundance, Shannon-Wiener diversity and evenness as well as diversity of realised species combinations were much higher than in any managed plot. This site also contained the largest amount and variation (tree species, size, decay phase) of dead wood. The bryophyte vegetation of the managed plots was much scarcer and much less diverse. These plots tended to contain very little dead wood of small size and early decay classes. These results are in agreement with the findings of comparative studies on managed and unmanaged boreal forests (Gustafsson and Hallingbäck 1988, Söderström 1988b, Lesica et al. 1991, Ohlson et al. 1997). The greatest difference was found in the diversity and abundance of dead wood inhabiting hepatics. Their occurrence is restricted to the habitats provided by large logs of intermediate to late decay phase, which are uncommon in managed stands (Söderström 1988b, Kruys et al. 1999). Among the managed stands the only exception was a recently thinned stand where the presence of fine woody debris supported a relatively high number of bryophytes including a few species inhabiting dead wood. Kruys and Jonsson (1999) studied the importance of fine woody debris in maintaining bryophyte diversity in managed spruce stands. They show that at low volumes of woody debris, species richness increased with the proportion of fine components, whereas at higher volumes with the proportion of coarse woody debris. These results also support the conservation value of dead wood resulting from tending. It is argued that successful maintenance of bryophyte diversity in Central European beech forests requires not only the preservation of the small isolated near-natural stands, but also a reasonable dead wood management in the matrix of commercial forests (Harmon 2001). Large and hence long lasting logs are crucial for providing appropriate establishment sites for the most sensitive hepatics that are rare habitat specialists with limited dispersal capacity (Söderström 1988a).

Among others, near-natural and managed stands in the investigated forest type mainly differ in that in managed stands the amount of CWD is lower and the age distribution of living trees is more even, resulting in more homogeneous light conditions. It is supposed that these differences in stand structure of near-natural and managed stands have an effect on both bryophyte and herbaceous understorey. However, their response to these conditions could be different, bryophytes are presumably more sensitive to the conditions of their potential substrates (Smith 1982b), while for vasculars the heterogeneity of light conditions could be more important (Bobiec 1988, Collins et al 1985). It is also unclear which descriptors of bryophyte and vascular vegetation are the most sensitive to the management induced stand structural differences (Boyle and Boontawee 1995, Bachmann et al. 1996).

Paper IV compares the diversity of bryophyte and vascular vegetation in the same stands as Paper III. In each stand, a 40 m x 40 m plot was selected, in which the vegetation was systematically sampled in 64 0.5 m x 0.5 m quadrats set out on a grid at 5 m intervals. In case of vascular species their cover, in case of bryophytes their local frequencies were registered in each quadrate. Different characteristics of diversity were calculated such as species richness, Shannon-Wiener diversity, Shannon-Wiener evenness and spatial heterogeneity (expressed as the variance of neighbouring quadrats). These descriptors were calculated at more spatial scale merging the data of neighbouring quadrats. Proportion, pattern and richness of potential substrate types determine the diversity of bryophytes. For all descriptors, the diversity was highest in the rocky site of the reserve, where the proportion of rocks and CWD is considerable, while the diversity of the other site of the reserve is similar to that of old managed stands. For vasculars, the diversity was similar in the two semi-natural stands, and much higher than in the managed ones. This means that vasculars are more sensitive to light conditions, which are more heterogeneous in the two near natural stands, than the diversity of substrates. These statements correspond to several studies emphasising the importance of light conditions to the diversity and pattern of woody herbs (Collins et al. 1985, Collins and Picket 1987, Diekmann 1994, Fekete 1974, Standovár 1998). In the case of both organism groups, the differences in spatial heterogeneity are more pronounced than in species richness and in diversity functions. Not only the values of the functions but also their spatial dependence was different among sites of high and low diversity. The reasons of the differences in values and spatial dependence of these indices are that in more diverse plots the

populations occur in fine grained spatial pattern, their patches or individuals are mixed with that of other populations, while in less diverse plots the populations occur in larger, monodominant (or species poor) patches. This is closely related to the spatial pattern of limiting (or differentiating) environmental conditions: (1) for bryophytes the heterogeneity of substrates is higher at fine spatial scale in the rocky reserve plot than in others, (2) for vasculars the heterogeneity of light conditions is higher at fine spatial scale in both plots of the reserve than in the managed plots.

These studies (Papers I-IV) make clear that the quantity and quality of dead wood are very important for the bryophyte vegetation of Central European montane beech stands. There are a lot of species that can live only on dead wood (obligate epixylics) and many species have become more common because of the presence of CWD (Paper I). Dead wood is also very important for diverse epilithic bryophyte assemblages due to humus accumulation among rocks (Paper II). Comparing the bryophyte vegetation of near-natural and managed stands, the diversity of the first was found to be much higher because of the larger amount and better quality (all decay phases are represented, large logs also occur) of CWD (Paper III-IV). Being aware of these facts, it becomes more and more important to study the ecology of dead wood inhabiting bryophytes. The most important questions of these studies are the following: (1) "How does the bryophyte composition of logs change during decay process?" – or asking this question from an other point of view – (2) "What are the preferences of species to different decay phases?"; (3) How much do the size of logs and microclimatic conditions modify these potential successional ways? In the temperate broad-leaved region, most bryological studies on dead wood follow the Braun-Blanquet concept of vegetation science describing epixylic communities (Barkman 1958; Hübschmann 1986; Marstaller 1986). Analysing habitat preferences of multi-species assemblages does not give detailed information on the ecological behaviour of bryophyte species growing on dead wood.

Paper V describes the preference of bryophytes for certain decay phases in dead wood. The effects of habitat type in near-natural beech stands and log size have also been included in this study. Two of the investigated beech stands represent the zonal beech forests (Bükk Mts.: Őserdő Forest Reserve, Keszthely Mts.: Tátika Forest Reserve), and another two the ravine-like beech forests, with a higher air humidity and higher amount of CWD (Mátra Mts.: Kékes North Forest Reserve, Bükk Mts.: Leány Forest Reserve). In each stand a plot was selected, in which the characteristics

of logs and their bryophyte floras were detected. Species preferences are analysed with a logistic regression model based on 1143 samples. A total of 30 bryophyte species were included in the analysis. During this analysis, the occurrence probability of a species is predicted on a log of a certain decay phase and a given volume in a certain site. This regression is not able to predict the occurrence probability of rare species.

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 these 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, where the thin logs fall on small and large boulders and stay free from the soil. Consequently, they are not buried and epixylics are able to colonise them. Furthermore, the competitive ability of epilithic species is not large enough to overgrow them. In zonal stands the logs are colonised by indifferent species or wide tolerant epixylics, and from the epixylic species only the most common ones are present. Thin logs become buried into the soil without bryophyte colonisation.

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 epixylics. The more common epixylic species have a wider tolerance to decay than 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 this effect is more important in zonal stands than in ravines. Common species have a high probability of occurrence on small logs. This leads indirectly to the conclusion that the bryophyte flora on small logs is species-poor and is dominated only 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 and Hallingbäck 1988, Andersson and Hytteborn 1991, Söderström 1988a, Paper III, Rambo and Muir 1998). Based on observed species responses, a simplified scheme for bryophyte succession on dead wood has

been developed. It is supposed that this unidirectional compositional process is carried out during very frequent extinction and establishment events (Jonsson and Söderström 1988a, Söderström and Jonsson 1989, Laaka-Lindberg 2000, Kimmerer 1993). It is expected that the actual species composition depends on the disturbance history of logs and the stochastic events of colonisation and extinction. Slow-growing liverworts and acrocarp mosses can only colonise gaps in the intact moss cover and open wood patches (Kimmerer, 1996), while fast growing pleurocarp mosses will build large patches in a short time.

Scientific and practical messages of the study

The goal of these studies is twofold: on one hand, they attempt to answer some scientific questions, but, on the other hand, they also aim at influencing the attitude of forest managers towards a more natural dead wood management. The most important scientific results of the thesis are the following:

(1) it gives a qualitative and quantitative description of the bryophyte vegetation of Kékes North Forest Reserve;

(2) it describes the interspecific relationships among species of outcrops and dead wood;

(3) it compares the sensitivity of different vegetation characteristics of vascular and bryophyte understory in managed and unmanaged stands;

(4) it classifies dead wood inhabiting bryophytes according to their preferences to decay phase, log size and habitat type, trying to show the potential successional ways in bryophyte vegetation during decay.

The most important message of the thesis for forest and conservation managers is that the diversity of bryophytes considerably depends on the quantity and quality of dead wood. The conservation of forest dwelling organisms is also a responsibility of forest managers: they should make a compromise between the force of timber production and ecological considerations. The protection of wildlife cannot be restricted to highly protected sites but it should also be extended to the managed stands (Hansen et al. 1991, Standovár and Primack 2001). There are plenty of possibilities to increase the amount of dead wood considering also the standpoints of management (Csóka 2000, Harmon 2001). In the case of "shelterwood management system", leaving alive a part of the trees after cutting can increase the amount of CWD and structural heterogeneity

in the following generations (Sódor 2000). The remaining fine woody debris after cleaning and selection cutting could be very important for bryophyte vegetation (Paper III, Kruys and Jonsson 1999). The occurrence of large logs is very important, their duration is longer, the extinction of local populations is lower on them, and the populations have more time to colonise them. During cutting there are some parts of the cut trees, which are not valuable economically, but they could be very important for biodiversity if they were left on the forest floor as dead wood (e.g. parts of crowns, damaged trunk parts). The "tree selection management system" can guarantee besides continuous timber production the continuous presence of uneven-aged stand structure and dead wood of different sizes and decay phases (Roth 1935). If the presence of CWD in different decay stages is continuous in time, it makes the survival of dispersal limited populations possible. Dead wood is a very important structural component of the forest, it is the habitat of many organisms (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). This study emphasises its importance only in terms of bryophytes.

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Summary

This thesis consists of five investigations concerning the bryophyte vegetation of semi-natural beech forests and the effects of coarse woody debris (CWD) on it. Although these papers are independent publications, they are in close contact with each other, representing different states of a uniform investigation.

Paper I gives a qualitative description about the bryoflora and bryophyte vegetation of Kékes North Forest Reserve. Abundance, ecological requirements, substrate specificity of the species are characterised. In the core area, 20 liverwort species and 48 moss species are found. In the background of this very high species richness, both the high environmental heterogeneity and naturalness of the reserve play a role. Although a species rich bryophyte vegetation can be found in the fissures of andesite outcrops in ravine like sites and on rock walls, the bryophyte vegetation occurring on decaying logs makes the reserve unique.

Paper II describes the same bryophyte vegetation as Paper I, but in a more quantitative way. It investigates the substrate specificity and interspecific relationships of the species. Frequent species of species poor bare rocks are separated from species rich assemblages of humus rich outcrops and coarse woody debris. There is an overlap between the species pool of humus rich outcrops and that of dead wood. The presence of CWD not only provided habitat for dead wood inhabiting bryophytes, but also resulted in diverse epilithic bryophyte assemblages on outcrops rich in humus. Observed number, diversity and evenness of species combinations are significantly lower, whereas spatial dependence (expressed as associatum) is significantly higher than under the neutral models even when data are stratified according to substrate types.

Paper III compares the diversity of bryophytes and the quantity and quality of CWD in Kékes North Forest Reserve with five neighbouring managed stands of different ages. From the reserve two plots were investigated representing considerably rocky and less rocky habitat types. The bryophyte vegetation was richer in the near-natural stands, especially in the moist rocky site. Species richness, abundance, Shannon-Wiener diversity and evenness as well as diversity of realised species combinations were much higher than in any managed plot. This site also contained the largest amount and variation (according to size and decay phases) of dead wood. The bryophyte vegetation of the managed plots was less diverse, these plots tended to

contain very little dead wood. The greatest difference was found in the diversity and abundance of dead wood inhabiting hepatics. It is argued that successful maintenance of bryophyte diversity in Central European beech forests requires a reasonable dead wood management in the matrix of commercial forests.

Paper IV compares the diversity of bryophyte and vascular vegetation in the same stands as Paper III. It investigates which descriptors of bryophyte and vascular vegetation are the most sensitive to the management induced stand structural differences. Different descriptors of diversity were calculated at more spatial scale. In case of bryophytes all descriptors of diversity were the highest in the rocky site of the reserve, while diversity of vasculars was similar in the two semi-natural stands, and much higher than in the managed ones. In the case of both organism groups the differences are more pronounced at spatial heterogeneity than species richness and diversity functions. Not only the values of the functions but also their spatial dependence was different among sites of high and low diversity. The background of the values and spatial dependence of these indices is that in more diverse plots the populations occur in fine grained spatial pattern, while in less diverse plots the populations occur in larger, monodominant (or species poor) patches. The diversity of bryophytes is determined by the diversity and spatial pattern of potential substrate types, while vasculars are more sensitive to light conditions.

Paper V describes the preference of bryophytes for certain decay phases in dead wood. The effects of habitat type (zonal or ravine like beech forests) in near-natural beech stands and log size have been included in this study. In the ravine-like forests more species are found and regionally rare epixylic species (mainly liverworts) are limited to these forests. In these 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. The species were classified into four categories on the basis of their preference to decay phases using regression analysis: epixylics, indifferent species, wide tolerant epixylics and epiphytes. The epixylics and wide tolerant epixylics prefer the latest decay phases. Wide tolerant epixylic species occur more often in earlier decay phases than epixylics. Indifferent species and wide tolerant epixylics are regionally common bryophytes, and they often grow on substrates other than dead wood. Generally the occurrence probabilities of species increase with log size, but its effect 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.

These studies emphasise for forest managers that the diversity of bryophytes considerably depends on the quantity and quality of dead wood. It is important to increase the amount of dead wood considering ecological and economical standpoints in managed stands, too. Although this study concentrates on bryophyte vegetation the presence of dead wood is essential for a lot of other organisms in forest.

Összefoglalás

Jelen dolgozat öt tanulmányon alapul, amelyek a természetközeli bükkösök mohavegetációjával, illetve a holt faanyag mohavegetációra gyakorolt hatásával foglalkoznak. Ezek az önálló tanulmányok egymással szoros tematikus kapcsolatban vannak, és egy egységes vizsgálat különböző lépéseit képviselik.

Az első dolgozat a Kékes Észak Erdőrezervátum mohavegetációjáról ad egy általános leírást, jellemezve az egyes fajok tömegességét, aljzatspecificitását és ökológiai igényeit. A területen 20 májmoha és 48 lombosmoha előfordulásáról számol be. E fajgazdag mohavegetáció kialakulásában az erdő termőhelyi heterogenitásának, valamint érintetlenségének egyaránt nagy szerepe van. Bár az andezit sziklafalak és sziklagörgetegek mohavegetációja is nagyon értékes, a korhadó fákon megjelenő mohagyepek teszik egyedivé a terület mohavegetációját.

A második dolgozat ugyanezen a területen kvantitatív módon vizsgálja a mohavegetáció szerkezetét, a fajok aljzatspecificitását, valamint a fajok közötti kapcsolatokat. A gyakori fajok között elkülönülnek a nyílt sziklafelszínek mohái a korhadó fák, valamint az árnyas sziklazugok moháitól, amelyek viszont jelentős mértékben átfednek egymással. A holt fák jelenléte nem csak a rajtuk kialakuló mohagyepek miatt jelentős, hanem növeli a sziklai mohavegetáció diverzitását, a sziklák közötti humusz felhalmozódása miatt. Aljazatonként külön vizsgálva a fajkombinációk száma, diverzitása, egyenletessége alacsonyabb, a fajok közötti térbeli függőség (asszociátum) értéke viszont magasabb a fajok véletlen kombinációihoz viszonyítva.

A harmadik dolgozat a mohavegetáció diverzitását, valamint a holt faanyag mennyiségét és minőségét hasonlítja a rezervátum sziklás és kevésbé sziklás termőhelye, valamint öt különböző korú, kezelt állomány között. A mohavegetáció diverzitása a rezervátumban jóval nagyobb, különösen a sziklás termőhelyen, mint a kezelt állományokban, mind a fajszám, tömegesség, Shannon-Wiener diverzitás, a fajkombinációk száma és a fajkombinációk diverzitása tekintetében. A rezervátum sziklás termőhelyén a holt fa mennyisége, valamint méret és korhadási fázis szerinti heterogenitása jóval nagyobb volt, mint a kevésbé diverz kezelt állományokban. A legnagyobb különbség a korhadéklakó májmohák tömegességében és sokféleségében jelentkezett. E vizsgálat megmutatja, hogy az erdei mohavegetáció diverzitásának

fenntartásához a gazdálkodás során gondoskodni kell a megfelelő mennyiségű és minőségű korhadó fáról a kezelt állományokban is.

A negyedik dolgozat ugyanezekben az állományokban tanulmányozza az edényes- és a mohavegetáció sokféleségét. Több térfolyamati lépésben vizsgálja, hogy a vegetáció milyen jellemzői a legérzékenyebbek a gazdálkodás okozta faállomány-szerkezeti különbségekre. Míg a mohák esetében minden változó a rezervátum sziklás termőhelyén érte el a legnagyobb értéket, addig az edényes vegetáció esetében mindkét természetközeli állomány hasonlóan diverznek mutatkozott, meghaladva a kezelt állományok értékeit. Mindkét csoport esetében a különbségek jóval nagyobbak voltak a vegetáció térbeli heterogenitását jellemző függvényeknél, mint a fajszám ill. faj-egyed diverzitás jellemzőinél. A magas és alacsony diverzitású állományok nem csak a függvények értékében, hanem azok térbeli léptékfüggésében is eltértek. Ennek hátterében az áll, hogy amíg a diverz állományokban a populációk finom szemcsés mintázatban fordulnak elő, addig a kevésbé diverzekben nagy kiterjedésű monodomináns (ill. fajszegény) foltok jelennek meg. A mohavegetáció elsősorban a potenciális aljzatok diverzitására és térbeli mintázatára érzékeny (kiemelkedik a rezervátum sziklás termőhelye), míg az edényesek diverzitását és mintázatát elsősorban a fényviszonyok határozzák meg (amelyek mindkét rezervátumi állományban nagy heterogenitást mutatnak).