

The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, Western Hungary

Flóra Tinya · Sára Márialigeti · Ildikó Király ·
Balázs Németh · Péter Ódor

Received: 27 August 2008 / Accepted: 17 December 2008 / Published online: 6 January 2009
© Springer Science+Business Media B.V. 2009

Abstract The effect of light on different understory plant groups (herbs, ground floor bryophytes, trunk-dwelling bryophytes and seedlings) was studied in a deciduous–coniferous mixed woodland in Western Hungary. The correlation of cover and species richness in each group and the cover of individual species to relative diffuse light were analyzed at different spatial scales. The study was carried out in 34 forest stands with different tree species composition. The importance of light in determining species composition was investigated by redundancy analysis. Species within each plant group were classified based on their light response. Light was positively correlated with species richness of herbs, cover of ground floor and trunk-dwelling bryophytes, and species richness and cover of seedlings. In redundancy analysis, the variance explained by light was 13.0% for herbs, 15.0% for bryophytes and 8.6% for seedlings. Within the group of herbs, species preferring open conditions and

light-flexible (gap) species were separated on the basis of the spatial scale of the analysis, while shade-tolerant species were not correlated positively with light. Among bryophytes mainly terricolous, opportunistic and mineral soil-inhabiting species showed significant positive correlations with light, while epiphytic and epixylic species did not respond to light. Seedlings of *Quercus petraea* and *Pinus sylvestris* were positively related to light, while most other seedling species were shade-tolerant. In case of vascular plants, the species' correlations with light were in agreement with their light indicator values; however, they were independent in the case of bryophytes. This study proved that the extent and spatial pattern of light influenced strongly the understory plant groups. Species within each group respond to light conditions differently, concerning the strength, direction and spatial scale of the relationships.

Keywords Relative diffuse light · Diversity · Composition · Environmental relationships · Epiphytes · Seedlings · Herbaceous plants · Light indicator values · Temperate mixed forests

Electronic supplementary material The online version of this article (doi:10.1007/s11258-008-9566-z) contains supplementary material, which is available to authorized users.

F. Tinya
Department of Plant Pathology, Corvinus University of
Budapest, Ménesi út 44, 1118 Budapest, Hungary

S. Márialigeti · I. Király · B. Németh · P. Ódor (✉)
Department of Plant Taxonomy and Ecology, Loránd
Eötvös University, Pázmány P. sétány 1/C,
1117 Budapest, Hungary
e-mail: ope@ludens.elte.hu

Introduction

In the understory vegetation of forests light is one of the most relevant environmental variables by influencing species abundance (Elemans 2004; Whigham 2004; Bartemucci et al. 2006), composition (Jelaska

et al. 2006) and diversity (Schmidt et al. 1996). Through the stand structure and tree species composition, the quantity, quality and pattern of light are strongly influenced by human management.

Optimal light conditions are obviously different for the understory species. Collins et al. (1985) distinguished among three types of forest herbs (sun, light-flexible and shade-tolerant) according to their response to gaps and light conditions. However, the number of quantitative studies concerning the light demands of European herbaceous species is very low (Mrotzek et al. 1996; Jelaska et al. 2006). Because, there are no scientific standards for the measurement of light in forests, our knowledge on the relationships between herb species and light and the classification of species into light response types are often unreliable. Barbier et al. (2008) emphasized the importance of classifying forest understory species based on their relationships to different abiotic factors (e.g. light) to promote understanding the effects of stand structure on the biodiversity of understory vegetation. An obstacle of a general classification is that light demands of species can change within their area.

Investigations focused on the effect of light on community characteristics gave variable results in particular studies. According to Bartemucci et al. (2006), light transmission was important for the cover and height of the understory vegetation, but it did not have strong influence on species composition and diversity. Härdtle et al. (2003) showed that the effects of light on the species richness of the understory depend on the type of the forest. However, other studies could not detect any effect of light on the forest understory (Collins and Pickett 1987; Augusto et al. 2003, Chen et al. 2004, Lenière and Houle 2006).

Information about the light requirements of forest bryophytes is even more limited. Their response to light can be different from many vascular plants, because they are evergreen. Although the light compensation point of forest interior bryophytes is generally low, light conditions in shaded forest can limit the growth of both terricolous and epiphytic species (Proctor 1982; Gabriel and Bates 2003). The most influential factors of forest bryophyte diversity and composition on stand-scale (5–20 ha) are the availability and heterogeneity of different microsites (disturbed patches, dead trunks and stumps, Mills and MacDonald 2004; von Oheimb et al. 2007).

However, the proportion of these microsites often correlates indirectly with light availability. Mills and MacDonald (2005) and Moora et al. (2007) found that within microsites (e.g. on undisturbed forest floor) light conditions were important to species composition. On the other hand, Humphrey et al. (2002) and Mills and MacDonald (2004) did not find significant relationship between light and bryophyte species richness. In case of epiphytic bryophyte assemblages, light proved to be an important factor affecting species composition and diversity both in the forest interior (Gustafsson and Eriksson 1995) and on pollarded trees standing on forested meadows (Moe and Botnen 1997).

There is more extensive research concerning the effects of light on growth and abundance of tree regeneration, because of its direct economical importance (Ke and Werger 1999; Finzi and Canham 2000; Godefroid et al. 2005). Insight into the light requirements of the tree regeneration is essential for forestry, especially when management is to be based on natural forest dynamics (Emborg 1998, Hunziker and Brang 2005).

As in temperate forests, natural regeneration is mainly based on fine scaled gap-dynamics, many studies investigated the effect of gaps on the microclimate (light, temperature, humidity, etc.) and on the woody and herbaceous understory (Collins and Pickett 1987, 1988; Schmidt et al. 1996; Emborg 1998; Schumann et al. 2003; Mihók et al. 2005). However, compared to gap studies, the information about the light conditions of closed forest stands is scarcer (Härdtle et al. 2003; Bartemucci et al. 2006; Jelaska et al. 2006).

Light demands of plant species can be ranked according to the light indicator values, e.g. applying the most widely used indicator value system developed by Ellenberg et al. (1992) for Central Europe. The indicator values are very useful for the description of ecological changes in monitoring studies (Grandin 2004; Samonil and Vrska 2008), for ecological comparison of floristically different areas (Roo-Zielinska 2003) or different management regimes (Dzwonko 2001; Decocq et al. 2004).

This investigation was focused on four plant groups of temperate mixed forests (herbs, bryophytes of the forest floor, bryophytes occurring on standing trees and tree and shrub seedlings). The objective of the study was to answer the following questions:

- (1) To what extent can the variation in species composition be explained by light?
- (2) To what extent are light conditions correlated with species richness and cover of different plant groups?
- (3) To what extent are light conditions correlated with cover of individual species?
- (4) How are these correlations related to the Ellenberg light indicator values of the species?
- (5) What is the role of the spatial scale in the response of herbs to light conditions?

Methods

Study area

The study area was located in the Órség National Park, Western Hungary (N 46°51′–55′ and W 16°07′–23′, ca 13 km × 24 km). The elevation is between 250 and 350 m above sea level and the topography consists of hills and wide valleys. Mean annual precipitation is 800 mm, mean yearly temperature is 9.1°C, and the western part of the region has a cooler and more humid climate than the eastern parts (Marosi and Somogyi

1990). The bedrock is alluviated gravel mixed with loess. The soil is acidic (pH 4.5–4.7 in the upper 20 cm, Szodfridt 1969) and nutrient poor, the most common soil type on hills is pseudogleyic brown forest soil, while in the valleys mire and meadow soils can be found (Stefanovits et al. 1998).

The forests of the region are dominated by beech (*Fagus sylvatica*), sessile and pedunculate oak (*Quercus petraea* et *Quercus robur*), hornbeam (*Carpinus betulus*), Scotch pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which occur in monospecific and mixed stands as well. The proportion of different mixing species (*Betula pendula*, *Populus tremula*, *Castanea sativa*, *Prunus avium*, etc.) is high (Tímár et al. 2002). Tree height varies between 20 and 30 m, living stock is 300–600 m³/ha, dead wood volume is 1–50 m³/ha (Table 1). Forest management is heterogeneous, both spontaneous stem selection system resulting in uneven aged stands and shelterwood management system with a rotation period of 70–110 years occur (Matthews 1991). The herbaceous vegetation is formed by mesophilic and acidophilic species, the shrub layer mainly consists of beech, hornbeam and the saplings of the mixing species. The cover of

Table 1 Mean, standard deviation (SD), minimum (MIN) and maximum (MAX) values of the investigated forest stand and understory variables based on 34 sites

Variables	Mean	SD	MIN	MAX
<i>Forest stand variables</i>				
Stand density (stems/ha)	602.3	289.9	263	1319
Tree species richness	5.73	1.86	3	10
Relative volume of oaks	0.35	0.33	0.01	0.96
Relative volume of beech and hornbeam	0.32	0.30	0.01	0.94
Relative volume of pine and spruce	0.31	0.28	0.00	0.83
Height of dominant trees (m)	25.2	3.62	19	32.9
Living wood volume (m ³ /ha)	474.0	119.4	264	680
Dead wood volume (m ³ /ha)	23.3	19.0	2	79
DIFN (%)	2.71	1.82	0.62	7.76
Variation coefficient of DIFN within stands	0.51	0.25	0.12	1.23
<i>Understory variables</i>				
Herb cover (%)	3.77	7.10	0.01	33.61
Species richness of herbs	20.7	13.5	3	49
Ground floor bryophyte cover (%)	2.49	4.31	0.17	22.02
Species richness of ground floor bryophytes	19.2	7.1	8	34
Trunk-dwelling bryophyte cover (%)	20.0	13.5	0.8	48.7
Species richness of trunk-dwelling bryophytes	14.5	5.0	6	29
Seedling cover (%)	3.36	3.90	0.09	20.50
Species richness of seedlings	9.73	4.36	3	18

Light and understory data are related to the scale of 30 × 30 m². DIFN: diffuse non-interceptance of light (relative diffuse light in percentage)

herbs and bryophytes and the level of tree regeneration are very variable among the stands (Table 1).

Data collection

Thirty-four stands were selected, representing different tree species combinations and stand structure (Table 1). Further criteria of site selection were as follows: dominant trees older than 70 years, more or less level slope, absence of water influence and spatial independence of sites (the distance was minimum 500 m between the stands). One block of $30 \times 30 \text{ m}^2$ (0.09 ha) was selected in a typical part of each stand. This represented the average openness of the overstory, and did not contain large gaps. Light characteristics and cover of herbs were measured in 36 adjoining $5 \times 5 \text{ m}^2$ plots in the blocks, between June and August 2006.

Relative diffuse light conditions (DIFN—diffuse non-interceptance, which represents the percentage of diffuse light coming through the canopy) were characterized using LAI-2000 Plant Canopy Analyzer (LI-COR Inc. 1992a). According to our previous study, this technique proved to be the best method to estimate relative light in these forests, as opposed to spatially explicit light models and the use of spherical densiometer (Tinya et al. 2009). Three instantaneous measurements were taken in the centre of each plot at 1.3 m height immediately after each other (within some seconds). Repeated measurements are not needed with this device. Measurements were carried out under different sky conditions, but always at dusk to avoid direct light getting into the sensor. A 270° view restrictor masked the portion of the sky containing the sun and the operator (LI-COR Inc 1992a). Reference above-canopy measurements were taken on nearby open fields.

Total absolute cover (in dm^2) of herb and seedling groups and the cover of species within the groups were estimated visually in each plot. Woody plants lower than 0.5 m height were considered as seedlings. We did not discriminate between *Q. petraea* and *Q. robur* (considering both as *Q. petraea*), and did not identify the subspecies within the *Rubus fruticosus* agg.

The two bryophyte groups were sampled in a different way. The cover of ground floor bryophytes, including specimens occurring on the soil and logs, was estimated similarly to herbs and seedlings in

each plot. The absolute cover (in dm^2) of bryophytes occurring on living trees (“trunk-dwelling bryophytes”) was estimated on every trunk with a diameter larger than 20 cm, between 0 and 1.5 m height.

Nomenclature follows Tutin et al. (1964–1993) for vascular plants, Hill et al. (2006) for mosses and Grolle and Long (2000) for liverworts.

Data analysis

DIFN was calculated from the measured light data for each $5 \times 5 \text{ m}^2$ plot with the 2000-90 Support Software (LI-COR Inc. 1992b). The relationships between light transmittance and the plant groups were explored both by univariate and multivariate analyses.

Spearman rank correlations were calculated between light transmittance and the total cover and species richness (number of species) of the different groups. Since DIFN data were not normally distributed (Kolmogorov–Smirnov test with Lilliefors correction), only non-parametric methods were applied (Zar 1999). These calculations were carried out at the spatial scale of the whole block ($30 \times 30 \text{ m}^2$).

The relationships between light transmittance and the cover of individual species were also analyzed by Spearman rank correlations. In case of bryophyte species, cover estimated on the ground floor and on the trunks was summarized, thus the two bryophyte groups were merged for the species level analysis, because many species occurred in both groups.

According to the preliminary results, the relationships between light and herbaceous species may be significantly influenced by spatial scale because of the various size of patches created by different species (Tinya et al. 2009). Therefore, herbaceous species were analyzed at five different spatial steps by merging 4, 9, 16 and 36 adjacent plots, thus giving spatial steps of 5×5 , 10×10 , 15×15 , 20×20 and $30 \times 30 \text{ m}^2$. For each spatial step, every stand was represented by only one sampling unit. Therefore, sample size was always the same (34, the number of stands), and only the extent (m^2) of the sampling unit was changing. Cover of each species was summarized and DIFN values were averaged for the merged plots. Hereby spatial autocorrelation between plots of the same block was avoided. The plots chosen for the analyses at smaller scales had a nested arrangement from the southwest corner of the

block, but they did not contain the marginal plots. This formation was independent from the pattern of plants within the block.

Bryophyte and seedling species were analyzed only at the spatial scale of the whole block ($30 \times 30 \text{ m}^2$). Seedlings were not abundant enough to make calculations on smaller spatial scales, and trunk-dwelling bryophytes were related to trees and not to plots, so that they could be analyzed only at block-level.

In each group, only those species that were frequent enough for the statistical procedures were analyzed individually. The minimum frequency value was 7 for herbs and seedlings and 6 for bryophytes on the scale of blocks. SPSS 14.0 and Statistica 7.1 were used for correlation analyses (SPSS Inc. 1989–2005; Statsoft 2006).

To investigate the effect of light on species composition, both indirect and direct ordinations were performed (Podani 2000). The same set of species was included in multivariate analysis as in correlation analysis, while the sampling units were represented by blocks ($30 \times 30 \text{ m}^2$). The two bryophyte groups were merged similarly to the species level investigation. Species data were \ln transformed in all cases. Based on the detrended correspondence analysis, the gradient length of axes was relatively short for all groups (<2 standard deviation units). Thus, linear relationships were supposed to exist between light and the cover of individual species, and redundancy analyses (RDA) were carried out as direct ordination (ter Braak and Šmilauer 2002), with light transmittance as the only explanatory variable. The significance of the variance explained by light was tested by Monte Carlo simulations (499 permutations of the species data, F -test, ter Braak and Šmilauer 2002). Computations were carried out with Canoco for Windows 4.5 (ter Braak and Šmilauer 2002).

In case of bryophytes, the relationships of species to light were compared between substrate preferences as determined specifically for the study area (Boros 1968; Smith 1982). As in Órség rocks and outcrops are lacking, some species (e.g. *Isoetecium alopecuroides*, *Metzgeria furcata*, etc.), which usually occur both on bark and rock, were considered here as epiphytic species. To investigate the relationship between species-light correlations and the light indicator values of the species (Ellenberg et al. 1992), Spearman rank correlation analyses were used for every group.

Results

Descriptive statistics

Altogether 259 species were registered: 128 herbaceous species, 90 bryophyte (73 occurring on the ground floor and 60 on trunks) and 41 seedling species. From these, 87 (31 herbs, 42 bryophytes and 14 seedlings) were frequent enough for further examinations.

The cover and species richness of the different plant groups (herbs, ground floor bryophytes, trunk-dwelling bryophytes and seedlings) in each block are shown in Table 1. The mean DIFN of the 34 blocks was $2.7 \pm 1.8\%$, and ranged from 0.6% to 7.7%. The variation coefficient of DIFN within blocks (representing the heterogeneity of light within stands) averaged 0.51 (range 0.12–1.23). The cover of different plant groups is extremely variable among blocks, ranging from 0% to 20% (ground floor bryophytes, seedlings), to 30% (herbs) and to 50% (trunk-dwelling bryophytes, Table 1). Electronic Supplement 1 contains the stand structure, composition, light, understory cover and species richness data of $30 \times 30 \text{ m}^2$ blocks and cover of the individual investigated species (in dm^2).

Relationships between light and understory community characteristics

The total herbaceous cover did not correlate significantly with light, while light and herbaceous species richness did show a significant relationship (Table 2). On the contrary, in the case of ground floor and trunk-dwelling bryophytes, total cover significantly positively correlated to light, while species richness did not. Both cover and species richness of seedlings showed a significant correlation with DIFN values. The first RDA canonical axis (reflecting light) explained 13% of the total variance for herbs, 15% for bryophytes and 9% for seedlings (Table 3), and according to Monte Carlo tests it differed significantly from the random references in all cases.

Response of individual understory species to light

Based on Spearman rank correlations calculated between light and the cover of individual species, all of the investigated groups (herbs, bryophytes and seedlings)

Table 2 Spearman rank correlation coefficients calculated between relative diffuse light (DIFN: diffuse non-interceptance of light) and the cover and species richness of each plant group at the scale of $30 \times 30 \text{ m}^2$

	Cover	Species richness
Herbs	0.249	0.343*
Ground floor bryophytes	0.554**	0.175
Trunk-dwelling bryophytes	0.405*	0.267
Seedlings	0.370*	0.398*

** $P < 0.01$, * $P < 0.05$

Table 3 Variance explained by relative light (DIFN: diffuse non-interceptance) from the total variance of species composition of different plant groups based on redundancy analysis

	Variance explained by light (%)	F
Herbs	13.0	4.78**
Bryophytes	15.0	5.66**
Seedlings	8.6	3.00*

Significance of the canonical axis was tested by Monte Carlo simulations (F-test)

** $P < 0.01$, * $P < 0.05$

could be divided into functional types according to the species' response to light (Tables 4, 5, 6).

Herbs could be divided in three types (Table 4). Species of the first type showed the strongest relationship with light at the 20×20 or $30 \times 30 \text{ m}^2$ scale (e.g. *Calamagrostis epigeios*, *Carex pallescens*), while species of the second type were related to light mainly at finer scales (10×10 or $15 \times 15 \text{ m}^2$, e.g. *Brachypodium sylvaticum*, *Mycelis muralis*). The third type consists of species without significant positive correlation with light (e.g. *Ajuga reptans*, *Oxalis acetosella*). Bryophyte species could be classified according to whether their correlation with light was significantly positive or non-significant (Table 5). Positively correlating species inhabited mainly soil or mineral soil, while the cover of species living on woody substrates usually did not correlate with light intensity. Seedlings of *Pinus sylvestris*, *Quercus petraea*, *Frangula alnus*, *Rhamnus catharticus* and *Pyrus pyraster* showed significantly positive correlations with light, while the seedlings of dominant mesophilous woodland trees (e.g. *Carpinus betulus*, *Fagus sylvatica*, etc.) and many shrubs did not (Table 6).

Table 4 Spearman rank correlation coefficients (r) between relative diffuse light (DIFN) and the cover of herbaceous species belonging to the different functional types

Species	r	Scale (m^2)
Species correlating at coarser spatial scales		
<i>Agrostis stolonifera</i>	0.474**	20×20
<i>Calamagrostis epigeios</i>	0.646**	30×30
<i>Carex pallescens</i>	0.486**	20×20
<i>Carex pilulifera</i>	0.433*	30×30
<i>Carex sylvatica</i>	0.379*	30×30
<i>Danthonia decumbens</i>	0.376*	30×30
<i>Deschampsia cespitosa</i>	0.450**	30×30
<i>Hieracium lachenalii</i>	0.432*	30×30
<i>Juncus effusus</i>	0.483**	30×30
<i>Melampyrum pratense</i>	0.698**	30×30
<i>Veronica officinalis</i>	0.464**	30×30
Species correlating at finer spatial scales		
<i>Brachypodium sylvaticum</i>	0.404*	15×15
<i>Fragaria vesca</i>	0.372*	10×10
<i>Luzula luzuloides</i>	0.386*	10×10
<i>Luzula pilosa</i>	0.578**	15×15
<i>Mycelis muralis</i>	0.469**	15×15
<i>Rubus fruticosus</i> agg.	0.458**	15×15
Positively non-correlating species		
<i>Ajuga reptans</i>	0.093	5×5
<i>Athyrium filix-femina</i>	0.186	5×5
<i>Dryopteris carthusiana</i>	0.200	15×15
<i>Dryopteris filix-mas</i>	-0.313	10×10
<i>Galeopsis pubescens</i>	0.197	15×15
<i>Galium odoratum</i>	-0.391*	30×30
<i>Galium rotundifolium</i>	0.273	15×15
<i>Hieracium murorum</i>	0.191	5×5
<i>Maianthemum bifolium</i>	-0.205	10×10
<i>Oxalis acetosella</i>	0.219	5×5
<i>Polygonatum multiflorum</i>	0.126	15×15
<i>Pteridium aquilinum</i>	0.148	5×5
<i>Sanicula europaea</i>	0.188	15×15
<i>Viola reichenbachiana</i>	0.176	15×15

Results are shown only at spatial scale in which the relationship was strongest

** $P < 0.01$, * $P < 0.05$

The Spearman rank correlation between light indicator values and herbaceous species-light correlations was significantly positive ($n = 30$, $r = 0.44$, $P = 0.012$). Herbs correlating with light

Table 5 Spearman rank correlation coefficients (*r*) between relative diffuse light (DIFN) and the cover of bryophyte species

Species	<i>r</i>	Substrate preference
Correlating species		
<i>Dicranella heteromalla</i>	0.509**	Mineral soil
<i>Dicranum montanum</i>	0.396*	Epiphytic
<i>Dicranum polysetum</i>	0.495**	Soil
<i>Dicranum scoparium</i>	0.363*	Opportunistic
<i>Hylocomium splendens</i>	0.360*	Soil
<i>Hypnum cupressiforme</i>	0.542**	Wood
<i>Leucobryum glaucum</i>	0.387*	Soil
<i>Platygyrium repens</i>	0.381*	Wood
<i>Pleurozium schreberi</i>	0.443**	Soil
<i>Pohlia nutans</i>	0.497**	Mineral soil
<i>Polytrichastrum formosum</i>	0.584**	Soil
<i>Pseudoscleropodium purum</i>	0.403*	Soil
<i>Ptilidium pulcherrimum</i>	0.477**	Epiphytic
Non-correlating species		
<i>Amblystegium serpens</i>	−0.075	Wood
<i>Atrichum undulatum</i>	0.195	Mineral soil
<i>Brachytectiastrum velutinum</i>	−0.013	Opportunistic
<i>Brachytectium rutabulum</i>	0.124	Opportunistic
<i>Brachytectium salebrosum</i>	−0.166	Wood
<i>Bryum rubens</i>	0.034	Mineral soil
<i>Ditrichum pallidum</i>	0.270	Mineral soil
<i>Eurhynchium angustirete</i>	0.027	Soil
<i>Fissidens taxifolius</i>	−0.212	Mineral soil
<i>Frullania dilatata</i>	0.220	Epiphytic
<i>Herzogiella seligeri</i>	0.005	Epixylic
<i>Homalia trichomanoides</i>	0.015	Epiphytic
<i>Isoetecium alopecurooides</i>	0.230	Epiphytic
<i>Lophocolea heterophylla</i>	0.089	Epixylic
<i>Metzgeria furcata</i>	−0.085	Epiphytic
<i>Orthotrichum affine</i>	−0.048	Epiphytic
<i>Orthotrichum pallens</i>	−0.109	Epiphytic
<i>Orthotrichum speciosum</i>	−0.127	Epiphytic
<i>Orthotrichum stramineum</i>	−0.096	Epiphytic
<i>Plagiomnium affine</i>	0.224	Soil
<i>Plagiomnium cuspidatum</i>	0.236	Wood
<i>Plagiothecium cavifolium</i>	0.190	Soil
<i>Plagiothecium denticulatum</i>	−0.071	Wood
<i>Plagiothecium laetum</i>	−0.001	Wood
<i>Plagiothecium nemorale</i>	0.113	Wood
<i>Radula complanata</i>	−0.090	Epiphytic
<i>Tetraphis pellucida</i>	−0.177	Epixylic

Table 5 continued

Species	<i>r</i>	Substrate preference
<i>Thuidium delicatulum</i>	0.106	Soil
<i>Ulota crispa</i>	0.138	Epiphytic

Absolute cover values of bryophyte species from the ground floor and from the trunks were merged

** *P* < 0.01, * *P* < 0.05

Table 6 Spearman rank correlation coefficients (*r*) between relative diffuse light (DIFN) and cover in the case of seedlings (including shrubs) at the spatial scale of 30 × 30 m²

Species	<i>r</i>
Correlating species	
<i>Frangula alnus</i>	0.452**
<i>Pinus sylvestris</i>	0.673**
<i>Pyrus pyraister</i>	0.350*
<i>Quercus petraea</i>	0.651**
<i>Rhamnus catharticus</i>	0.412*
Non-correlating species	
<i>Acer pseudoplatanus</i>	−0.311
<i>Carpinus betulus</i>	0.212
<i>Castanea sativa</i>	−0.205
<i>Corylus avellana</i>	−0.115
<i>Crataegus monogyna</i>	−0.258
<i>Fagus sylvatica</i>	0.128
<i>Picea abies</i>	−0.309
<i>Prunus avium</i>	−0.309
<i>Prunus spinosa</i>	−0.191

** *P* < 0.01, * *P* < 0.05

at larger scales have a high L-value (usually between 5 and 8, Fig. 1a). However, species related to light at finer scales and positively non-correlating species have usually lower indicator values (between 1 and 4). The light indicator values of bryophytes and seedlings did not correlate significantly with species-light correlations (*n* = 42, *r* = 0.05, *P* = 0.742, Fig. 1b, and *n* = 14, *r* = 0.40, *P* = 0.157, Fig. 1c, respectively), however, in case of seedlings most of the significantly correlating species had higher (6–7) indicator values than the non-correlating ones (3–4).

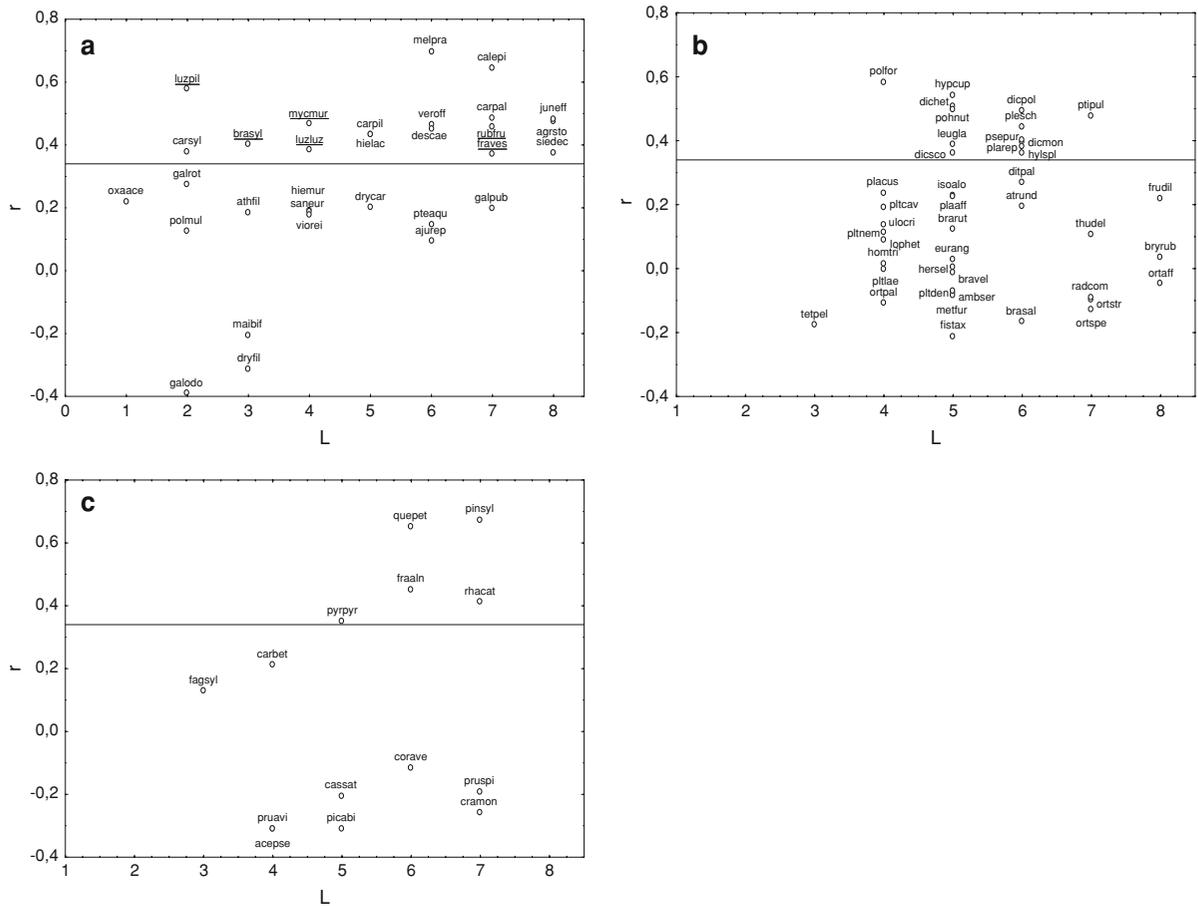


Fig. 1 Spearman rank correlation coefficients of species with relative diffuse light (r) plotted against their Ellenberg light indicator values (L). **a** Herbaceous plants, **b** bryophytes and **c**

seedlings. Horizontal line represents $P < 0.05$ significance level of correlation coefficients of species. In the case of herbs (**a**) species correlating at fine spatial scale are underlined

Discussion

General considerations

Our study revealed significant relationships between light and the studied plant groups. The extent and spatial pattern of light are crucial for the development of the understory vegetation. The relationship of the community characteristics (i.e. cover and species richness) with light conditions differs between plant groups. The various responses of individual species to light (according to strength and spatial scale) allowed to classify the species in distinct groups. The response of vascular plant species to light agreed with their light indicator values, but this was not the case for bryophytes.

In the redundancy analyses, light explained a relatively high proportion (8.6–15.0%) of the variance. Other studies found much lower explaining power even for the most important forest variables. In Danish beech forests, the maximal variation explained by one variable (age of the beech stand) was 6.4% for vascular plants and mosses (Aude and Lawesson 1998) and 5.96% for epiphytic species composition (Aude and Poulsen 2000). Among herbs and bryophytes, the cover of the dominant species correlated with light intensity, explaining a higher proportion of the total variance in the RDA. On the contrary, the most common species of seedlings (hornbeam and beech) are shade-tolerant, so light had a lower explaining power for this group.

Detection of the effect of light on forest understory is not always easy. Beside some technical questions (validity of a single instantaneous measurement at larger spatial and temporal scales, weather conditions and diffuse vs. direct light), the effect of other environmental variables on cover, species richness and composition of the studied plant groups must be also considered. Such variables are forest continuity (Verheyen et al. 2003; Winter and Möller 2008), colonization dynamics (Brunet and von Oheimb 1998; Bossuyt et al. 1999), management changes in the past (Moe and Botnen 1997; Bartemucci et al. 2006), forest community types (Fekete 1974; Draskovits and Ábrányi 1981, Härdtle et al. 2003) and abiotic factors influenced by stand structure, such as soil or microclimate.

Soil conditions and topography were more decisive for understory vegetation than light in many cases (Collins and Pickett 1987; Augusto et al. 2003, Lenière and Houle 2006). In the study of Chen et al. (2004), most of the understory species proved to be shade-tolerant, so the effect of nutrient and humidity was more important for the vegetation composition than light. Thomsen et al. (2005) found that understory species composition was primarily determined by indirect factors (such as light availability) of the overstory, but topographical, anthropogenic and spatial factors were similarly significant.

Herbaceous species

The species richness of herbs significantly correlated with light, contrary to their cover. A potential explanation of this could be that the nutrient poor, acidic soil limits the establishment of herbaceous cover independently of light. However, in lighter patches, more species are able to settle and survive. By analyzing the same plot data by generalized linear models, Ódor et al. (2007) found that light is an important variable in explaining herbaceous species richness, unlike cover. Standovár et al. (2006) and Moora et al. (2007) also found that the pattern diversity (beta diversity between plots of the same community, Magurran 2004) of understory vegetation was more sensitive to stand structural characteristics than cover. On the contrary, Bartemucci et al. (2006) found that the functional variables (e.g. height) of the herb layer were more sensitive to light than species richness or composition.

Investigating the response of individual species to light, species correlating with light could be divided into two finer categories according to scale. These functional types are similar to those of Collins et al. (1985), who divided understory herbs into sun, light-flexible and shade-tolerant species.

Some of the correlating species showed the strongest relationship with light at larger spatial scales (20 × 20 or 30 × 30 m²). This category is very similar to the “sun species” group of Collins et al. (1985), but the group is not uniform. Most of them are not typically forest species, because they live in wet meadows (e.g. *Agrostis stolonifera*, *Juncus effusus*, *Deschampsia cespitosa*), or clearcuts (e.g. *Calamagrostis epigeios*). They usually did not occur in deep shade, because they need large, continuous open areas. Their Ellenberg light values are high, which shows that they are considered to be species related to high light intensity. This functional type includes also many species which prefer acidic forest sites (e.g. *Veronica officinalis*, *Hieracium lachenalii*). Because in the studied region acidic forests are mainly open pine stands, their significant positive correlations with light are likely the results of indirect relationships.

The other type of correlating species (e.g. *Brachypodium sylvaticum*, *Mycelis muralis*) also showed significant correlations with light, but at finer spatial scales (10 × 10 or 15 × 15 m²), which is similar to the scale of individual gaps created by one or some trees in temperate forests (Kenderes et al. 2008). This type, similarly to the “light-flexible” species of Collins et al. (1985), contains typical forest species, which can survive at low DIFN values, but they become more abundant in gaps than under closed canopy. Most members of this type were considered earlier as species of closed forests (Wulf 2003), and their Ellenberg L-values are mainly low.

The group of positively non-correlating taxa was not homogeneous. Most of these species preferred shady plots and were absent or occurred only with small abundance at larger light intensity (e.g. *Galium odoratum*, *Oxalis acetosella*). They were also known previously as shade-tolerant species (Wulf 2003), and they have, in general, a low Ellenberg L-value. Some other species (e.g. *Dryopteris carthusiana*, *Galeopsis pubescens*) did not show significant correlation with light, but they had moderately larger cover at opener areas, and thus they can be related to light to a certain extent.

Therefore, it can be stated that herbaceous species are not similar according to the strength and spatial scale of their response to light. Moreover, the relationship between light and understory variables is very complex, and simple rules cannot be stated. This can cause contradictions between different studies—results depend on the used spatial scale and the type of the dominant species from the point of view of their light requirements.

Bryophytes

Forest-dwelling bryophytes are considered to be shade-tolerant. Their evergreen body has an extended photosynthetic activity in the vegetation period, and they are less dependent on the summer density of the overstory than herbs. Therefore, we expected a weaker relationship between bryophyte cover and light than for other plant groups (Proctor 1982; Gabriel and Bates 2003). However, in the RDA light explained higher proportion of variance for bryophytes than for herbs and seedlings.

For both ground floor and trunk-dwelling bryophytes, total cover correlated significantly with light, while species richness did not. Humphrey et al. (2002) and Mills and MacDonald (2004) did not find any relationship between light and species richness of bryophytes either. In the analysis of ground floor bryophyte assemblages of the same plots, Márialigeti (2007) found that light did not influence bryophyte species richness, but it was one of the most relevant explanatory variables for their cover. Species richness was related mainly to the diversity of substrates, similar to other forest types (Jonsson and Esseen 1990; Frisvoll and Presto 1997, Mills and McDonald 2004, von Oheimb et al. 2007). The species composition of epiphytic bryophytes is considerably influenced by tree species composition. Therefore, diversity of host species can increase epiphyte diversity (Schmitt and Slack 1990; Szövényi et al. 2004). Regarding the effect of more background variables on the trunk-dwelling bryophytes of these blocks, tree species composition was the most important factor for species richness: pine had very low, while oaks had high epiphyte diversity (Király 2008). This is in agreement with Heilmann-Clausen et al. (2005), who also found tree species diversity an important variable for bryophyte species richness.

However, bryophyte cover was constituted mainly by a few dominant species (e.g. *Polytrichastrum formosum*, *Pleurozium schreberi* on ground floor and *Hypnum cupressiforme* on trunks), which were related to light. In Irish spruce plantations, trees exposed to light had significantly higher epiphyte cover than those in the interior, while their diversity was similar (Coote et al. 2007).

On species level, in our study species significantly correlating with light and non-correlating species differed mainly in their substrate preference. Many terricolous and mineral soil-inhabiting species showed positive correlation with light (e.g. *Dicranella heteromalla*, *Polytrichastrum formosum*). This result may be an indirect effect of microsite heterogeneity, because in more open stands dominated by pine and oak the proportion of open soil surface is higher than in beech and hornbeam dominated stands. Another considerably limiting factor of these species is the amount of deciduous litter, which is negatively correlated with light. However, both shading and chemical allelopathic effects of deciduous litter significantly limit the growth of terricolous bryophytes (Startsev et al. 2008).

On the contrary to terricolous species, bryophytes species living on woody substrate did not correlate with light significantly. They are much more influenced by the availability of the required substrate (bark of the adequate tree species or dead wood in the preferred decay stages). *Hypnum cupressiforme* is an exception, because it usually occurs on wood, but it was strongly correlated with light. However, this species is not a substrate specialist: it can occur on any type of substrates. For many epiphytic bryophytes, high air humidity characteristic of closed stands is more important than light availability (Barkmann 1958).

In this study, the correlation of species with light was independent of their Ellenberg light values. There are two potential explanations of this phenomenon: (1) the spatial distribution of these species is mainly determined by other microhabitat factors, and they can tolerate a wide range of light conditions and (2) the light indicator values of bryophytes are less firmly established than those of herbs. Moreover, we have to consider that light was measured at the height of 1.3 m, which is considerably higher than bryophyte layer, and vascular plants under this level could reduce the incident light for ground floor bryophytes.

Seedlings of trees and shrubs

Species richness and cover of seedlings positively correlated with light, because in more open stands many mixing species could appear with high abundance.

Among seedlings of tree species only that species (*Pinus sylvestris* and *Quercus petraea*) correlated significantly with light, which also maintain open stands as overstorey species. They are known to be light-flexible species (with high Ellenberg light values), so our results are in agreement with the results of previous studies (Farque et al. 2001). Other tree seedling species, which compose dark, closed forests in the overstorey, did not respond to light. *Fagus sylvatica*, *Carpinus betulus*, *Acer pseudoplatanus*, *Castanea sativa* and *Prunus avium* were always considered as shade-tolerant species (Ellenberg et al. 1992).

In case of most investigated shrub species, strong correlations were expected, since they were considered as typical pioneer, light-demanding species of open areas (abandoned meadows and thickets), and therefore had also high indicator values. However, they proved to be quite different according to their light demands. *Rhamnus catharticus* and *Fraxinus alnus* correlated positively with DIFN value, so their abundance probably depends on the amount of light. The dispersal by birds of *Prunus spinosa* and *Crataegus monogyna* could be more important in their open condition preference than their light demands, as they can also survive under closed canopy. All correlating seedlings showed the strongest correlation at coarse scales.

Acknowledgements The authors thank Ákos Molnár, Zsuzsa Mag and István Mazál for field assistance, Tibor Standovár for the instruments and advice, Barbara Mihók for her suggestions and János Podani for reviewing an earlier version of the manuscript. This study was supported by the OTKA D46045, NI68218 and the Directory of Ország National Park. Péter Ódor is a grantee of the János Bolyai Scholarship.

References

- Aude E, Lawesson JE (1998) Vegetation in Danish beech forests: the importance of soil, microclimate and management factors, evaluated by variation partitioning. *Plant Ecol* 134:53–65. doi:10.1023/A:1009720206762
- Aude E, Poulsen RS (2000) Influence of management on the species composition of epiphytic cryptogams in Danish beech forests. *Appl Veg Sci* 3:81–88. doi:10.2307/1478921
- Augusto L, Dupouey JL, Ranger J (2003) Effects of tree species on understorey vegetation and environmental conditions in temperate forests. *Ann Sci* 60:823–831. doi:10.1051/forest:2003077
- Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understorey vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. *For Ecol Manage* 254:1–15
- Barkmann JJ (1958) Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum, Assen
- Bartemucci P, Messier C, Canham CD (2006) Overstorey influences on light attenuation patterns and understorey plant community diversity and composition in southern boreal forests of Quebec. *Can J Res* 36:2065–2079. doi:10.1139/X06-088
- Boros Á (1968) Bryogeographie und bryoflora ungarans. Akadémiai Kiadó, Budapest
- Bossuyt B, Hermy M, Deckers J (1999) Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. *J Ecol* 87:628–638. doi:10.1046/j.1365-2745.1999.00379.x
- Brunet J, von Oheimb G (1998) Migration of vascular plants to secondary woodlands in southern Sweden. *J Ecol* 86:429–438. doi:10.1046/j.1365-2745.1998.00269.x
- Chen HYH, Legare S, Bergeron Y (2004) Variation of the understorey composition and diversity along a gradient of productivity in *Populus tremuloides* stands of northern British Columbia, Canada. *Can J Bot* 82:1314–1323. doi:10.1139/b04-086
- Collins BS, Pickett STA (1987) Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. *Vegetatio* 70:3–10
- Collins BS, Pickett STA (1988) Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J Ecol* 76:437–450. doi:10.2307/2260604
- Collins BS, Dunne KP, Pickett STA (1985) Responses of forest herbs to canopy gaps. In: Pickett STA (ed) *The ecology of natural disturbance and patch dynamics*. Academic Press Inc., London, pp 218–234
- Coote L, Smith GF, Kelly DL, O'Donoghue S, Dowding P, Iremonger S, Mitchell FJG (2007) Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. *Biodivers Conserv* 16:4009–4024. doi:10.1007/s10531-007-9203-5
- Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Watez-Franger A, De Foucault B, Delelis-Dusollier A, Bardat J (2004) Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. *J Appl Ecol* 41:1065–1079. doi:10.1111/j.0021-8901.2004.00960.x
- Draskovits RM, Ábrányi A (1981) Effect of the illumination in different types of forests. *Ann Univ Sci Bud* 22–23:65–70
- Dzwonko Z (2001) Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *J Appl Ecol* 38:942–951. doi:10.1046/j.1365-2664.2001.00649.x
- Elemans M (2004) Light, nutrients and the growth of herbaceous forest species. *Acta Oecol* 26:197–202. doi:10.1016/j.actao.2004.05.003

- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa (indicator values of plants in Central Europe, in German). *Scr Geobotanica* 18:1–258
- Emborg J (1998) Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For Ecol Manage* 106:83–95
- Farque L, Sinoquet H, Colin F (2001) Canopy structure and light interception in *Quercus petraea* seedlings in relation to light regime and plant density. *Tree Physiol* 21:1257–1267
- Fekete G (1974) Tölgyesek relatív megvilágítása és gyepszint-fajainak eloszlása (relative light intensity and distributions of herb layer species in oakwoods). *Acta Bot Hung* 9:87–97 (in Hungarian)
- Finzi AC, Canham CD (2000) Sapling growth in response to light and nitrogen availability in a southern New England forest. *For Ecol Manage* 131:153–165
- Frisvoll AA, Presto T (1997) Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. *Ecography* 20:3–18. doi:10.1111/j.1600-0587.1997.tb00342.x
- Gabriel R, Bates JW (2003) Responses of photosynthesis to irradiance in bryophytes of the Azores laurel forest. *J Bryol* 25:101–105
- Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understorey in Belgium. *For Ecol Manage* 210:91–105
- Grandin U (2004) Dynamics of understorey vegetation in boreal forests: experiences from Swedish integrated monitoring sites. *For Ecol Manage* 195:45–55
- Grolle R, Long DG (2000) An annotated check-list of the hepaticae and anthocerotae of Europe and Macaronesia. *J Bryol* 22:103–140
- Gustafsson L, Eriksson I (1995) Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *J Appl Ecol* 32:412–424. doi:10.2307/2405107
- Härdtle W, von Oheimb G, Westphal C (2003) The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). *For Ecol Manage* 182:327–338
- Heilmann-Clausen J, Aude E, Christensen M (2005) Cryptogam communities on decaying deciduous wood—does tree species diversity matter? *Biodivers Conserv* 14:2061–2078. doi:10.1007/s10531-004-4284-x
- Hill MO, Bell N, Bruggeman-Nannaenga MA, Brugges M, Cano MJ, Enroth J, Flatberg KI, Frahm JP, Gallego MT, Gariletti R, Guerra J, Hedenas L, Holyoak DT, Hyvönen J, Ignatov MS, Lara F, Mazimpaka V, Munoz J, Söderström L (2006) An annotated checklist of the mosses of Europe and Macaronesia. *J Bryol* 28:198–267. doi:10.1179/174328206X119998
- Humphrey JW, Davey S, Peace AJ, Ferris R, Harding K (2002) Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biol Conserv* 107:165–180. doi:10.1016/S0006-3207(02)00057-5
- Hunziker U, Brang P (2005) Microsite patterns of conifer seedling establishment and growth in a mixed stand in the southern Alps. *For Ecol Manage* 210:67–79
- Jelaska SD, Antonic O, Bozic M, Krizan J, Kusan V (2006) Responses of forest herbs to available understorey light measured with hemispherical photographs in silver fir-beech forest in Croatia. *Ecol Modell* 194:209–218. doi:10.1016/j.ecolmodel.2005.10.013
- Jonsson BG, Esseen P-A (1990) Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *J Ecol* 78:924–936. doi:10.2307/2260943
- Ke G, Werger MJA (1999) Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. *Acta Oecol* 20:579–586. doi:10.1016/S1146-609X(99)00103-4
- Kenderes K, Mihók B, Standovár T (2008) Thirty years of gap dynamics in a Central European beech forest reserve. *Forestry* 81:111–123. doi:10.1093/forestry/cpn001
- Király I (2008) A faállomány változásainak hatása az Őrségi erdők kéreglakó mohaközösségére (The effect of stand structure to the epiphytic bryophyte assemblages in forests of Őrség region, West Hungary). MS Thesis, Loránd Eötvös University, Budapest (in Hungarian)
- Lenière A, Houle G (2006) Response of herbaceous plant diversity to reduced structural diversity in maple-dominated (*Acer saccharum* Marsh.) forests managed for sap extraction. *For Ecol Manage* 231:94–104
- LI-COR Inc (1992a) LAI-2000 plant canopy analyzer instruction manual. LI-COR Inc., Lincoln
- LI-COR Inc (1992b) 2000-90 Support software for the LAI-2000 plant canopy analyzer. LI-COR Inc., Lincoln
- Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford
- Marosi S, Somogyi S (1990) Cadastre of Hungarian regions, in Hungarian. MTA Földrajztudományi Kutató Intézet, Budapest (in Hungarian)
- Matthews JD (1991) Silvicultural systems. Calderon Press, Oxford
- Márialigeti S (2007) Faállomány—és egyéb környezeti változók hatása a mohavegetációra az Őrségi erdőkben (The effects of stand structure and other abiotic variables to the bryophyte vegetation in forests of Őrség region, West Hungary). M.Sc. Thesis, Loránd Eötvös University, Budapest (in Hungarian)
- Mihók B, Gálhidy L, Kelemen K, Standovár T (2005) Study of gap-phase regeneration in a managed beech forest: relations between tree regeneration and light, substrate features and cover of ground vegetation. *Acta Silv Lign Hung* 1:25–38
- Mills SE, MacDonald SE (2004) Predictors of moss and liverwort species diversity of microsites in conifer-dominated boreal forest. *J Veg Sci* 15:189–198. doi:10.1658/1100-9233(2004)015[0189:POMALS]2.0.CO;2
- Mills SE, MacDonald SE (2005) Factors influencing bryophyte assemblage at different scales in the Western Canadian boreal forest. *Bryologist* 108:86–100. doi:10.1639/0007-2745(2005)108[86:FIBAAD]2.0.CO;2
- Moe B, Botnen A (1997) A quantitative study of the epiphytic vegetation on pollarded trunks of *Fraxinus excelsior* at Havra, Osteroy, western Norway. *Plant Ecol* 129:157–177. doi:10.1023/A:1009720132726

- Moora M, Daniell T, Kalle H, Liira J, Pussa K, Roosaluuste E, Opik M, Wheatley R, Zobel M (2007) Spatial pattern and species richness of boreonemoral forest understorey and its determinants—a comparison of differently managed forests. *For Ecol Manage* 250:64–70
- Mrotzek R, Perona L, Schmidt W (1996) Einfluss von Licht und ausgewählten Bodenfaktoren auf die Verteilung von *Urtica dioica* L. und *Mercurialis perennis* L. in der Bodenvegetation des Buchenwaldökosystems der Fallstudie Zierenberg. *Verh Ges Ökologie* 26:559–564
- Ódor P, Mag Z, Márialigeti S, Tinya F, Németh B, Mazál I (2007) Effect of stand structure and tree species composition on different organism groups. In: International conference on natural hazards and natural disturbances in mountain forests, Trento, Italy
- Podani J (2000) Introduction to the exploration of multivariate biological data. Backhuys Publishers, Leiden
- Proctor MCF (1982) Physiological ecology: water relations, light and temperature responses, carbon balance. In: Smith AJE (ed) *Bryophyte ecology*. Chapman and Hall, London, New York, pp 333–382
- Roo-Zielinska E (2003) Ecological groups of vascular plant species in the herb layer of the pine forests of Northern and Central Europe. *Pol J Ecol* 51:493–506
- Samonil P, Vrska T (2008) Long-term vegetation dynamics in the Sumava Mts. natural spruce-fir-beech forests. *Plant Ecol* 196:197–214. doi:10.1007/s11258-007-9345-2
- Schmidt W, Weitemeier M, Holzapfel C (1996) Vegetation dynamics in canopy gaps of a beech forest on limestone—the influence of the light gradient on species richness. *Verh Ges Ökologie* 25:253–260
- Schmitt CK, Slack NG (1990) Host specificity of epiphytic lichens and bryophytes: a comparison of the Adirondack Mountains (New York) and the Southern Blue Ridge Mountains (North Carolina). *Bryologist* 93(3):257–274. doi:10.2307/3243509
- Schumann ME, White AS, Witham JW (2003) The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. *For Ecol Manage* 176:543–561
- Smith AJE (1982) *Bryophyte ecology*. Chapman and Hall, London
- SPSS Inc (1989–2005) SPSS 14.0 for Windows. Release 14.0.0
- Standovár T, Ódor P, Aszalós R, Gálhidy L (2006) Sensitivity of ground layer vegetation diversity descriptors in indicating forest naturalness. *Community Ecol* 7:199–209. doi:10.1556/ComEc.7.2006.2.7
- Startsev N, Lieffers VJ, Landhausser SM (2008) Effects of leaf litter on the growth of boreal feather mosses: implication for forest floor development. *J Veg Sci* 19:253–260
- Statsoft I (2006) Statistica version 7.1. www.statsoft.com
- Stefanovits P, Filep Gy, Füleki Gy (1998) Talajtan (soil science). Mezőgazda Kiadó, Budapest (in Hungarian)
- Szodfridt I (1969) Adatok az Órség erdőinek termőhelyi adottságaihoz (Data to the soil characteristics of the forests of Órség). *Vasi Szemle* 23:386–394 (in Hungarian)
- Szövényi P, Hock Z, Tóth Z (2004) Phorophyte preferences of epiphytic bryophytes in a stream valley in the Carpathian Basin. *J Bryol* 26:137–146. doi:10.1179/037366804225021092
- ter Braak CJ, Šmilauer P (2002) Canoco 4.5. Biometris. Wageningen and Ceske Budejovice
- Thomsen RP, Svenning JC, Balslev H (2005) Overstorey control of understorey species composition in a near-natural temperate broadleaved forest in Denmark. *Plant Ecol* 181:113–126. doi:10.1007/s11258-005-3996-7
- Tímár G, Ódor P, Bodoncz L (2002) Az Órségi Tájvédelmi Körzet erdeinek jellemzése (the characteristics of forest vegetation of the Órség landscape protected area). *Kanitzia* 10:109–136 (in Hungarian)
- Tinya F, Mihók B, Márialigeti S, Németh B, Mazál I, Mag Z, Ódor P (2009) A comparison of three indirect methods for estimating understorey light at different spatial scales in temperate mixed forests. *Community Ecol* (in press)
- Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA (1964–1993) *Flora Europea*. Cambridge University Press, Cambridge
- Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *J Ecol* 91:563–577. doi:10.1046/j.1365-2745.2003.00789.x
- von Oheimb G, Friedel A, Bertsch A, Härdtle W (2007) The effects of windthrow on plant species richness in a Central European beech forest. *Plant Ecol* 191:47–65. doi:10.1007/s11258-006-9213-5
- Whigham DF (2004) Ecology of woodland herbs in temperate deciduous forests. *Ann Rev Ecol Evol* 35:583–621. doi:10.1146/annurev.ecolsys.35.021103.105708
- Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. *For Ecol Manage* 255:1251–1261
- Wulf M (2003) Preference of plant species for woodlands with differing habitat continuities. *Flora* 198:444–460
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall, New Jersey