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Environmental factors structuring bryophyte species composition in block fields in south-western Moravia (Czech Republic)

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KUBEŠOVÁ S. 2010: Environmental factors structuring bryophyte species composition in block fields in south-western Moravia (Czech Republic). *Acta Musei Moraviae, Scientiae biologicae* (Brno) **95(2):** 55–70. – An inventory of bryophytes was made in 23 naturally treeless block fields in the Oslava, Jihlava, Jevišovka and Dyje river valleys of south-western Moravia (Czech Republic). Environmental variables such as potential direct irradiation, area, position on the slope, stone size and degree of stone sorting were recorded in each block field. Block fields were divided into two different zones: a central, open part and an ecotone between the block field and adjacent woodland. The total number of species was 88 (20 liverworts and 68 mosses). Bryophyte cover was lower in the open part than in the ecotone. Variability of species data, as revealed by detrended correspondence analysis, was associated with position on slopes, potential direct irradiation and position in the gradient between open part and ecotone. The most frequent life strategies were colonists and perennials. Colonists were characteristic of the open parts and of more insolated sites. Long-lived shuttles and perennials occurred more often at edges and on lower slopes. Among the growth-forms, rough mats and short turfs were the most frequent. The most insolated habitats were inhabited by small cushions, tails and short turfs. Thalloid mats and dendroids were typical of the sites that were situated on lower parts of the slopes, in lower ecotones and at less insolated sites. The most frequent phytogeographical affinities of the recorded species were temperate, boreal and sub-boreal.

Key words. growth-forms, bryophytes, life strategies, chorological types, south-western Moravia, block fields

Introduction

Block fields represent an azonal habitat type in Central Europe (MOLENDA 1999), usually forming habitat islands that can conserve unique ecosystems and relict organisms (SÁDLO & KOLBEK 1994, BRABEC & CÍLEK 1998). Several extrazonal bryophyte occurrences have been recorded in block fields (e.g. in the Czech Republic, Germany). LÜTH (1999) recorded the arctic-alpine moss *Gymnomitrion concinnatum* in a block field at an altitude of 600 m, and NĚMCOVÁ (2000) found *Gymnomitrion corallioides*, *G. concinnatum* and four other arctic-alpine bryophytes (330–650 m) here.

The bryophyte species composition in block fields and similar habitats may be influenced by a number of environmental factors, such as presence of tree canopy (KUBEŠOVÁ 2000, NĚMCOVÁ 2001), insolation (aspect), soil factors (COX & LARSON 1993a,b, NĚMCOVÁ 2001) and rock-fall disturbances (LARSON *et al.* 1989). The bryophyte assemblage also depends on relative position within the block field: lower parts are usually more humid and are subject to more cold air movement. Altitude also plays a critical part (LÜTH 1999).

In the Czech Republic, the bryophyte flora of block-field habitats has been described by PUJMANOVÁ (1989, 1990), NĚMCOVÁ (2000, 2001) and KUBEŠOVÁ (2002). However, growth-forms and life strategies were not analysed in them.

Each growth-form and life strategy is related to a more or less distinct and characteristic range of environmental conditions (GIMINGHAM & BIRSE 1957, BIRSE 1957, 1958a,b, KÜRSCHNER *et al.* 1998). A recognisable group of species (growth-forms or life strategies in this case) even provides better indication value of habitat conditions than species composition (GIMINGHAM & BIRSE 1957). Block fields possess a variety of habitats with different microclimates and substrates (KUBEŠOVÁ 2000). The microclimate can be influenced by air movement within the body of the block field (KUBÁT 1974, WUNDER & MÖSELER 1996, HACHTEL *et al.* 1999). Bryophyte growth-forms and life strategies should reflect this variety and microclimate.

The aim of this paper is to analyse (1) how environmental factors influence species composition in block fields in south-western Moravia and (2) which environmental factors are important for various functional types and phytogeographical groups of bryophytes.

Materials and Methods

Study sites

Data were collected in 23 block fields in south-western Moravia, Czech Republic (Fig. 1). These block fields are located in the valleys of the Oslava, Jihlava, Jevišovka and Dyje rivers, which are deeply incised in a gently undulating plateau (CULEK 1996). Elevations range between 240 m and 430 m and block field area varies between 100 m^2 and 7000 m^2. They are situated on slopes at 35–50° (–60°) inclination. The block fields are formed by acidic rocks, including cleaved granite, granulite, gneiss, and orthogneiss (MATĚJOVSKÁ 1991, BATÍK 1992). Most of the stones have diameters between 20 cm and 300 cm and are relatively stable, with occasional stone movement occurring only in the upper parts of some study sites. The mean air temperature in January is between -2°C and 4°C, in July between 17°C and 18°C. Precipitation during the winter season (October–March) ranges between 200 mm and 300 mm and in the growing season (April–September) between 350 mm and 450 mm (data from 1901–1950; QUITT 1971, 1975).

Recording of environmental variables

The following environmental variables were recorded in each block field:

- the potential direct irradiation – calculated as the sum of relative values of potential direct irradiation for seven days (December 21, January 21, February 21, March 21, April 21, May 21 and June 21) according to HERBEN (2003); aspect and slope were used as input variables for the calculation
- the phytogeographical location – thermophyticum (warm and dry region) or mesophyticum (moderately cool and dry region) (SKALICKÝ 1988) were recorded

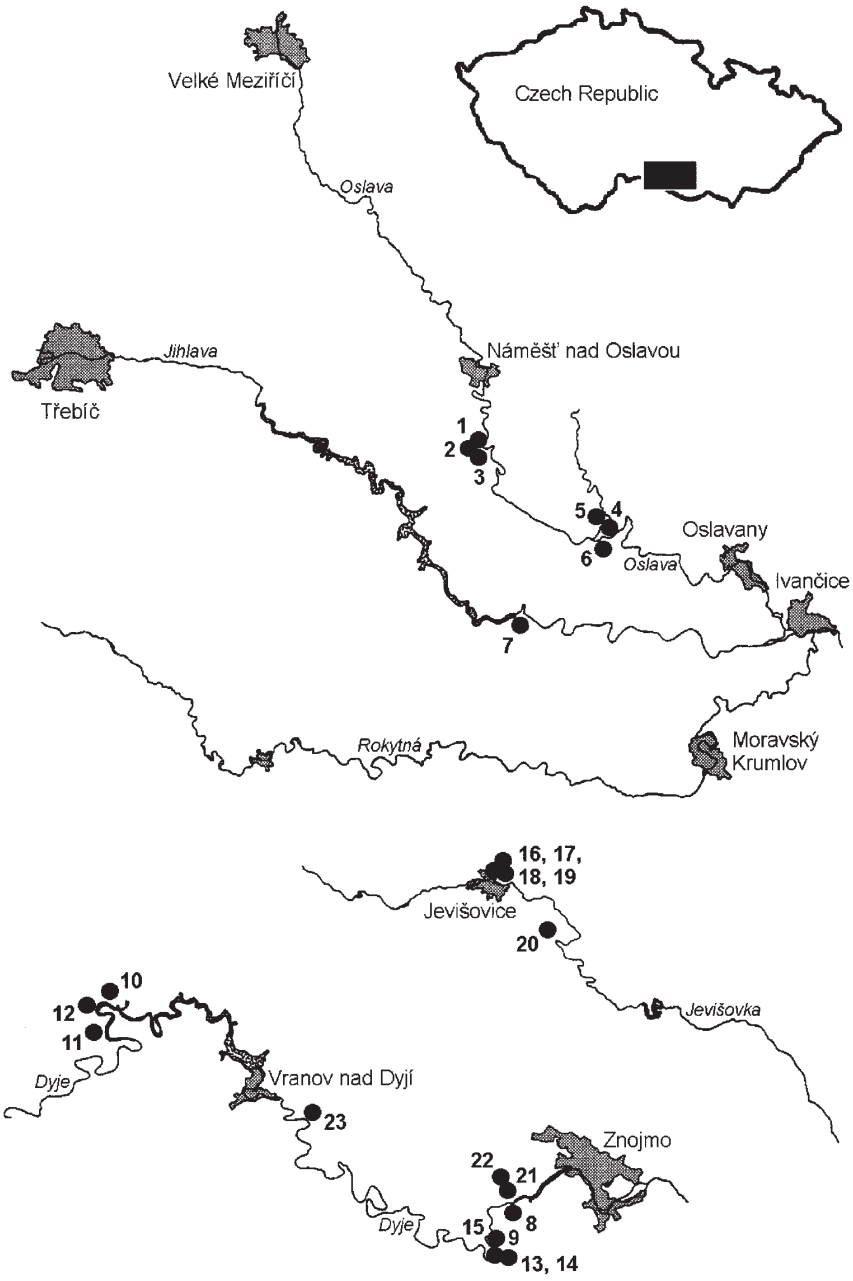


Fig. 1. Location of the study sites.

- the position on slope – a nominal variable with three categories, expressing block field location in the upper, middle or lower part of the slope
- the area – estimated using the ordinal scale: 1 (<500 m^2), 2 (500–2500 m^2), 3 (>2500 m^2)
- the mean size of stones – using the ordinal scale: 1 (30 cm), 2 (30–50 cm), 3 (50 cm)
- the degree of stone sorting – estimated using a three-point scale: 0 (no sorting distinguishable; size of stones similar in upper and lower parts of the block field), 1 (moderate sorting), 2 (distinctive sorting; small stones in upper part and large stones accumulated in lower part).
- open central part and ecotone – block fields were divided into two different zones: the open central part and the ecotone, the latter being further subdivided into upper and lower ecotone. The ecotone (fringe) consisted of the marginal part of a block field shaded by adjacent forest canopy (and demarcated by the vertical projection of the tree canopy). Unlike the open central part, the ecotone contained more litter in the cavities between boulders.

Recording of bryophytes

- the cover of the bryophyte layer – recorded in each block field separately for the open part and the upper and lower ecotones
- the presence of bryophyte species – recorded in each block field separately for the open part and the upper and lower ecotones; bryophyte abundance and cover were estimated using an ordinal scale (1 – rare, 2 – scattered, 3 – frequent and 4 – dominant)
- growth-forms – categories defined on the basis of plant architecture; the system of growth-form types presented by DURING (1990) which is based on systems by GIMINGHAM & BIRSE (1957) and MÄGDEFRAU (1982) was employed
- life-strategy categories – after DIERßEN (2001), a system which is based on DURING (1992)
- chorological types – after DÜLL (1983, 1984, 1985).

Nomenclature of species follows FREY *et al.* (1995) with the exception of *Plagiothecium curvifolium* Schlieph. ex Limpr.

Data analysis

The Mann-Whitney U-test was used for testing bryophyte cover differences between the open central part and the ecotone (not divided into upper and lower part).

Detrended correspondence analysis (DCA) of bryophyte species was carried out with abundance and cover expressed on an ordinal scale, using the Canoco program (TER BRAAK & ŠMILAUER 1998). As the variation in species composition within individual block fields was considerable, data from each block field were separated into three sets:

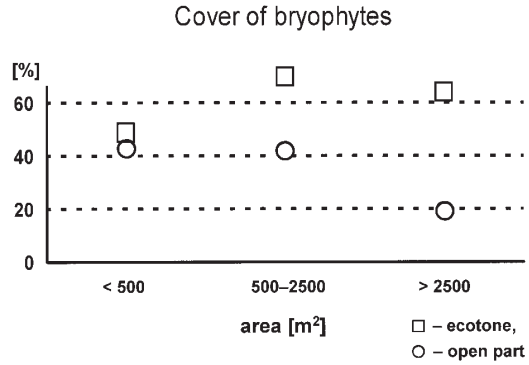


Fig. 2. Mean cover of bryophytes in 23 block fields of south-western Moravia.

species recorded (1) in the central open part, (2) in the upper ecotone, and (3) in the lower ecotone. Each of these data sets was analysed separately. Environmental variables were projected as passive onto the DCA ordination diagram.

Some of the block fields studied were situated close to each other, forming five apparent clusters (Fig. 1). Therefore the codes 1–5 for individual clusters were used as co-variables so as to remove the effect of similarity of nearby sites. DCAs of life strategies, growth-forms and chorological types were made in the same way, with consideration, however, to the proportion of species. The sub-Mediterranean-suboceanic type occurred at only one site and was excluded from DCA.

Results

In 23 block fields 88 species were recorded, made up of 20 liverworts and 68 mosses. The most frequent species in terms of number of localities and abundance in the block fields were *Dicranum scoparium* (100% of localities), *Hypnum cupressiforme* (100%), *Polytrichum formosum* (95%), *Hedwigia ciliata* (91%), *Pohlia nutans* (91%), *Grimmia ovalis* (74%), *Pleurozium schreberi* (69%), and *Barbilophozia barbata* (65%).

Cover of bryophytes was lower in the open central part of the block fields (thus: south-facing slopes – 25%, n = 5, north-facing slopes – 34%, n = 11) than in the ecotone (thus: south-facing ecotones – 56%, n = 5, north-facing ecotones – 65%, n = 11). The difference in cover between the open central part and the ecotone (of all block fields, n = 23) was significant (Mann-Whitney U-test, U = 90.5, p = 0.0003). It was higher in the open, central part of small block fields than in large ones (Fig. 2). The difference between the open central part and the ecotone grew with increasing area.

The bryophytes *Isothecium alopecuroides*, *Metzgeria furcata* and *Paraleucobryum longifolium* were typical of block fields situated in the lower part of slopes (Figs 3, 4).

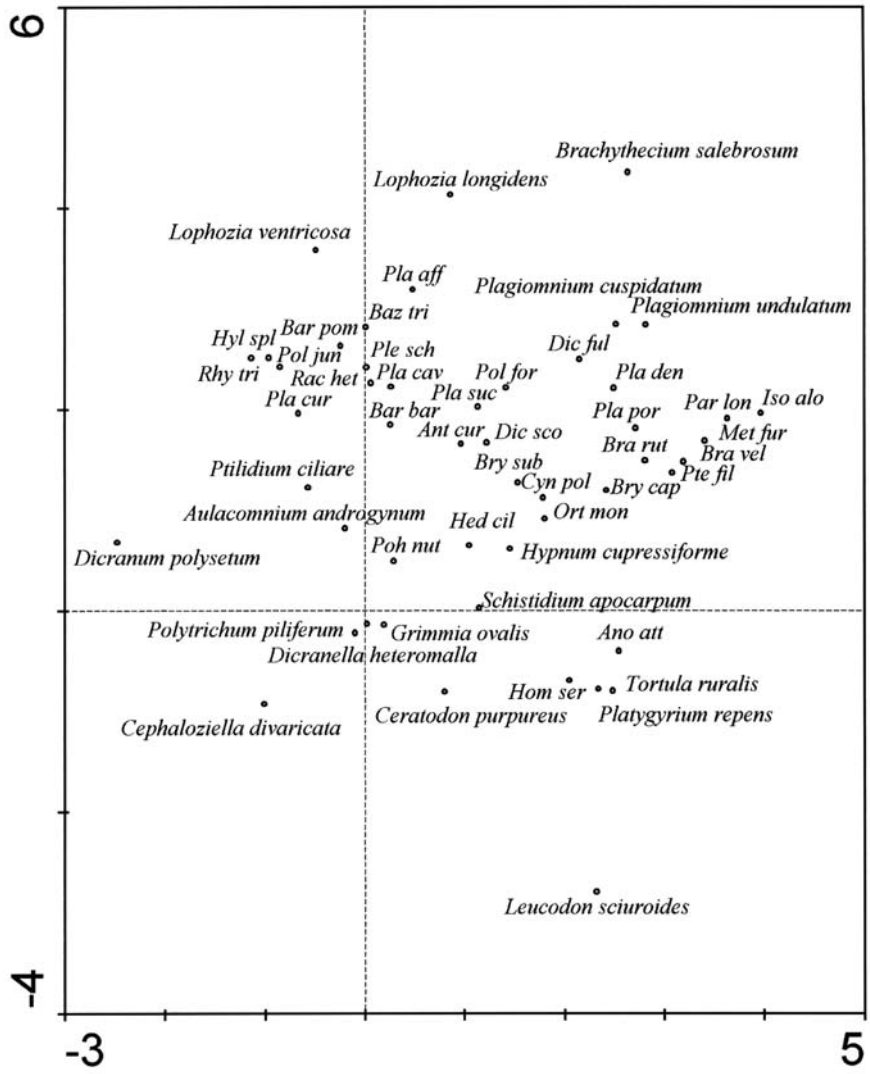


Fig. 3. DCA ordination diagram, species plot of bryophytes in 23 block fields in south-western Moravia. Anoatt – *Anomodon attenuatus*, Antcur – *Antitrichia curtipendula*, Barbar – *Barbilophozia barbata*, Barpom – *Bartramia pomiformis*, Baztri – *Bazzania trilobata*, Brarut – *Brachythecium rutabulum*, Bravel – *B. velutinum*, Brycap – *Bryum capillare*, Brysub – *B. subelegans*, Cynpol – *Cynodontium polycarpon*, Dicful – *Dicranum fulvum*, Dicsco – *D. scoparium*, Hedcil – *Hedwigia ciliata*, Homser – *Homalothecium sericeum*, Hylspl – *Hylocomium splendens*, Isoalo – *Isothecium alopecuroides*, Metfur – *Metzgeria furcata*, Ortmon – *Orthodicranum montanum*, Parlon – *Paraleucobryum longifoium*, Plaaff – *Plagiomnium affine*, Placav – *Plagiothecium cavifolium*, Placur – *P. curvifolium*, Pladen – *P. denticulatum*, Plapor – *Plagiochila porelloides*, Plasuc – *Plagiothecium succulentum*, Plesch – *Pleurozium schreberi*, Pohnut – *Pohlia nutans*, Polfor – *Polytrichum formosum*, Poljun – *P. juniperinum*, Ptefil – *Pterigynandrum filiforme*, Rachet – *Racomitrium heterostichum*, Rhytri – *Rhytidiadelphus triquetrus*. Axis 1 – horizontal, axis 2 – vertical.

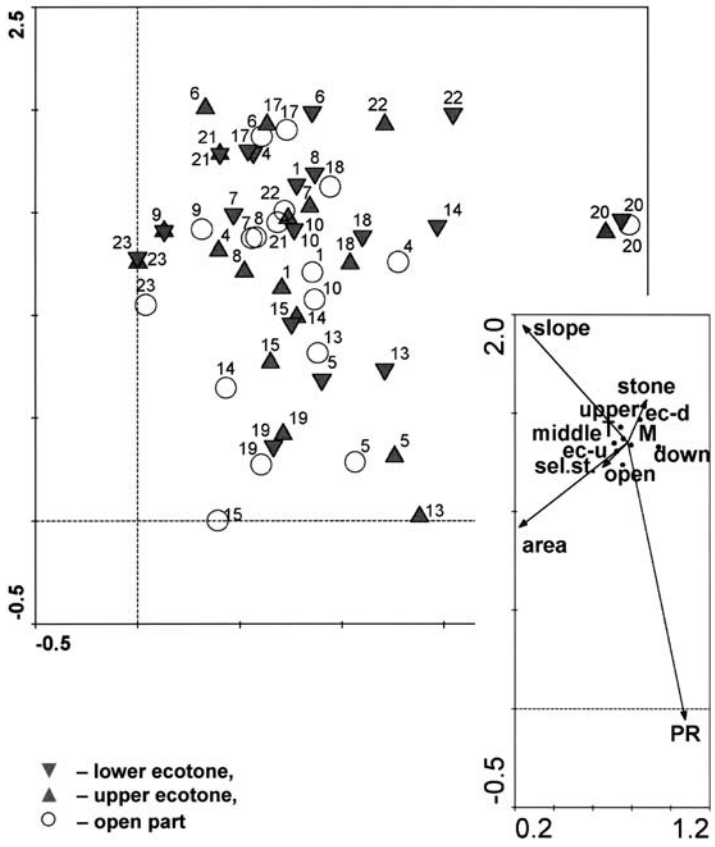


Fig. 4. DCA ordination diagram showing position of individual block field zones and environmental factors, south-western Moravia. 1–23 – no. of block field, ec-d – lower ecotone, ec-u – upper ecotone, M – mesophyticum, PR – potential direct irradiation, s.st. – sorting of stones, stone – size of stones, T – thermophyticum. Axis 1 – horizontal, axis 2 – vertical.

Cephaloziella divaricata, *Ceratodon purpureus*, *Homalothecium sericeum*, *Leucodon sciuroides*, *Platygyrium repens* and *Tortula ruralis* were characteristic of block fields with high potential solar irradiation. The liverworts *Bazzania trilobata*, *Lophozia longidens*, *L. ventricosa* and the mosses *Bartramia pomiformis* and *Plagiomnium affine* prevailed in block fields with low potential direct irradiation values.

The cumulative percentage variances for the first two DCA axes of species data were 14% and 24%. Variability along the first axis arose out of different positions of the block fields on slopes, contrasting lower parts to central parts of valley slopes (Fig. 4). A complex of environmental factors associated with radiation resulted in variability along

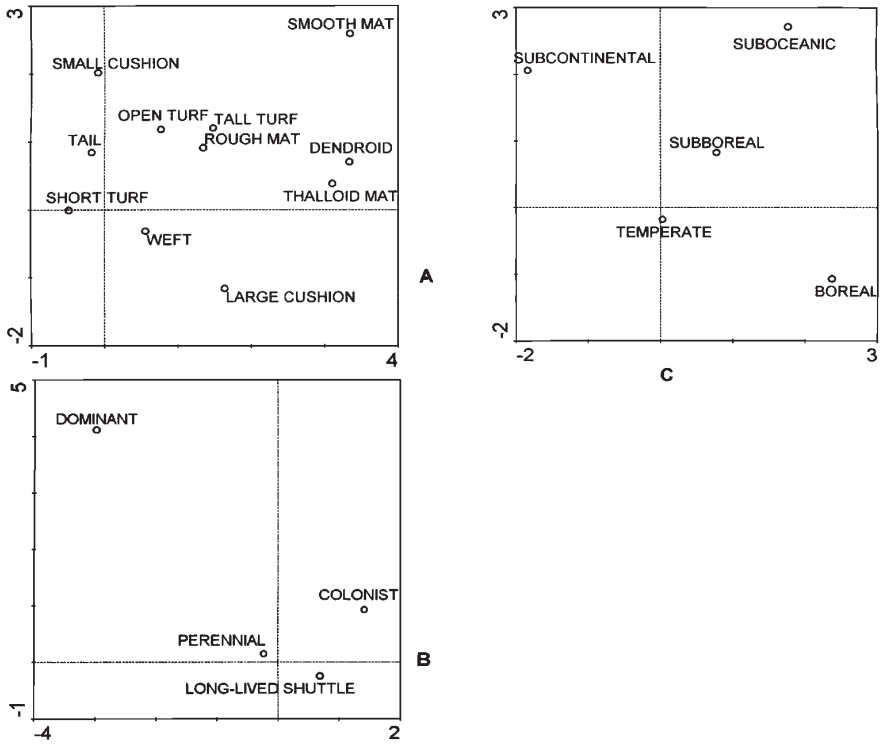


Fig. 5. DCA ordination diagrams showing position of (A) growth forms, (B) life strategies and (C) chorological types of bryophytes in 23 block fields, south-western Moravia, Czech Republic. Axis 1 – horizontal, axis 2 – vertical.

the second axis, but differences between the open central part and the ecotone and between small and large stones were also correlated with this second axis.

Similarities between various parts of the same block field were more frequent than those of open parts or ecotones over different block fields (Fig. 4). Open parts and ecotones were less similar in larger block fields and more similar in smaller block fields.

Growth-forms: rough mats and short turfs were the most frequent, while cushions, tails, tall turfs and wefts were less frequent. Dendroids, open turfs, smooth and thallus mats were rare in the block fields. The cumulative percentage variances for the first two axes of growth-form data were 25% and 38% (Fig. 5). The main variability along the first axis was associated with potential direct irradiation. The most insolated habitats were inhabited by small cushions, tails and short turfs. Small cushions occurred especially in the open central parts. Two growth-forms – thalloid mat and dendroid – were typical of less insolated, lower ecotones, situated in the lower part of the slope.

Life strategies: the most frequent were colonists and perennials (perennials, competitive perennials and stress-tolerant perennials), while dominants, fugitives and long-lived shuttles were infrequent. The fugitive strategy occurred on one site only and was consequently excluded from the analysis. The cumulative percentages variance for the first two axes of life-strategy data were 46% and 62% (Fig. 5). Potential direct irradiation was associated with the first axis of ordination. The colonist (s. lat.) strategy was found to be characteristic of open parts of the block fields and of more insolated sites. Both colonists (s. str.) and colonist pioneers occurred frequently, but colonists (s. str.) were rarer. Dominants were typical in lower ecotones and in block fields with less potential direct irradiation. Long-lived shuttles and perennials occurred more often at edges and in block fields that were situated in the lower part of the slope.

Chorological types: temperate, boreal and sub-boreal were the most frequent, while suboceanic, subcontinental and sub-Mediterranean-suboceanic species were less frequent in the block fields. The cumulative percentage variances for the first two axes of the chorotypes were 47% and 67% (Fig. 5). Distribution of chorotypes along the first axis reflected values of potential direct irradiation and the complex of dependent variables.

Discussion

Potential direct irradiation

Insolation appeared to be the most important factor influencing the distribution of bryophyte diversity in block fields. It is evident that potential irradiation represents a complex of related environmental factors, including humidity and temperature. It was correlated with a lower cover of bryophytes in the open central part of south-facing block fields. Němcová (2001), who studied basalt, phonolite and trachyte talus slopes in northern Bohemia, also recorded the lowest number of species largely on south-facing slopes and on smaller taluses.

In addition to the bryophytes that are generally confined to drier and half-shaded-to-sunny habitats, the epiphytic species *Leucodon sciuroides* and *Platygyrium repens* were characteristic of the most insolated block fields. The presence of epiphytic species was due to fallen branches, wood debris and litter at the margins of the block fields. The moss *P. repens* occurs most frequently on oaks (Pospíšil 1985), which often border more insolated block fields (thermophilous oak forests in the upper parts of the slope; Chytrý & Vicherek 1995, 1996).

Potential irradiation was also the determining factor for growth-forms, life strategies and chorological types in block fields. In terms of growth-forms, small cushions, tails and short turfs inhabited the more insolated block fields. The high insolation there led to a drier, extreme environment that small cushions and short turfs were able to tolerate. Generally, exposed conditions are characterised by xerotolerant cushions and short turfs (Gimingham & Birse 1957, Schofield 1981, Mägdefrau 1982, Smith 1982, Kürschner *et al.* 1998, Kürschner 1999).

The more insolated block fields were settled with colonists s. lat. (ephemeral and pioneer colonists). It has been demonstrated in several studies of other habitats that

colonists prefer open sites (e.g. Orbán 1989, During 1992). They were most frequent at the driest sites in forests (González-Mancebo & Hernández-García 1996), where they often occurred on bare rocks (During 1979). Both strategies, colonists *sensu stricto* and colonist pioneers, were recorded in block fields, but colonist pioneers were rarer. Generally, colonists inhabit open but potentially productive habitats, in contrast to colonist pioneers, which are able to grow in very harsh environments and are common at the earliest stages of successions (During 1992).

The distribution of chorological types was associated with decreasing values of irradiation (and the complex of dependent variables). The subcontinental and temperate types preferred more insolated sites and sub-boreal, suboceanic and boreal types preferred shaded sites. Similarly, the boreal type (bryophytes, lichens and vascular plants) has been recorded more often on north-facing scree slopes in eastern Belgium (Weddeling & Hachtel 2000).

Open part and ecotone

The differences between the two block field zones – open part and ecotone – were marked in terms of bryophyte cover. The extent of the bryophyte layer in the ecotone was related to tree shade and relative air humidity.

The presence of some bryophyte groups was also strongly influenced by this environmental pattern. The colonist (s. lat.) life strategy and the small cushion growth-form preferred the drier, open parts of the block field, whereas long-lived shuttles and perennials preferred the more humid ecotone. Similarly, Orbán (1989), González-Mancebo & Hernández-García (1996) and Kürschner & Parolly (1998) mentioned higher frequencies of perennials and long-lived shuttles on more humid sites. These perennial strategies are typical of more or less constant environments (During 1979), which make them better adapted to the more moderate microclimate of the ecotone (compared with the open block field part) (Halfmann 1991, Němcová 2001). The dominant strategy and the thalloid mat and dendroid growth-forms were confined to lower ecotones. These block field parts are moist and relatively cold (e.g. Wunder & Möseler 1996). Gimingham & Birse (1957) and Schofield (1981) mentioned dendroid and thalloid mats exhibiting preference for shaded and humid sites.

Position on slope

The position of the block field on the slope was also important. Variability along the first DCA axis was associated with the various positions of block fields on slopes – lower parts and central parts of valley slope. Topographic shading, as discussed in Chytrý & Tichý (1998), can influence the environmental conditions of the block field, especially on lower slopes. Typical bryophytes of the lower slopes were the shade-tolerant species *Isothecium alopecuroides*, *Metzgeria furcata* and *Paraleucobryum longifolium*.

Long-lived shuttles and perennials occurred as more frequent life strategies on lower slopes. The life span of these strategy types ranges from a few to many years (During 1992), and they occur in more or less constant environments (During 1979). In the study area, they preferred more stable habitats such as shaded block field edges at the foot of

slopes. The thalloid mat and dendroid growth-forms were confined to lower slope parts. Generally, mats are limited to sites where moisture is available (SCHOFIELD 1981) and block fields in the lower parts of slopes seem to be moist and relatively colder. A cold microclimate in the lower parts of block fields was revealed by measurement at several sites (WUNDER & MÖSELER 1996, MÖSELER & WUNDER 1999, NĚMCOVÁ 2001).

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References

BATÍK P. 1992: *Geologic map of the Podyjí National park.* Český geologický ústav, Praha (in Czech).

BIRSE E.M. 1957: Ecological studies on growth-form in bryophytes. II. Experimental studies on growth-form in mosses. *Journal of Ecology* **45:** 721–733.

BIRSE E.M. 1958a: Ecological studies on growth-form in bryophytes. III. The relationship between growth-form of mosses and ground-water supply. *Journal of Ecology* **46:** 9–27.

BIRSE E.M. 1958b: Ecological studies on growth-form in bryophytes. IV. Growth-form distribution in a deciduous wood. *Journal of Ecology* **46:** 29–42.

BRABEC E. & CÍLEK V. 1998: *Ekologie sutí Českého středohoří. Kritická recenze a přehled výsledků.* Pp. 49–59. In: CÍLEK V. & KOPECKÝ J. (eds.): *Pískovcový fenomén: klima, život a reliéf.* Česká speleologická společnost, Praha, Broumov, 174 pp (in Czech).

CHYTRÝ M. & TICHÝ L. 1998: Phenological mapping in a topographically complex landscape by combining field survey with an irradiation model. *Applied Vegetation Science* **1:** 225–232.

CHYTRÝ M. & VICHEREK J. 1995: *Lesní vegetace Národního parku Podyjí / Thayatal. Die Waldvegetation des Nationalparks Podyjí / Thayatal.* Academia, Praha, 166 pp (in Czech and German).

CHYTRÝ M. & VICHEREK J. 1996: Přirozená a polopřirozená vegetace údolí řek Oslavy, Jihlavy a Rokytné. *Přírodovědný Sborník Západomoravského Muzea v Třebíči* **22:** 1–124 (in Czech).

COX J.E. & LARSON D.W. 1993a: Environmental relations of the bryophytic and vascular components of a talus slope plant community. *Journal of Vegetation Science* **4:** 553–560.

COX J.E. & LARSON D.W. 1993b: Spatial heterogenity of vegetation and environmental factors on talus slopes of the Niagara Escarpment. *Canadian Journal of Botany* **71:** 323–332.

CULEK M. (ed.) 1996: *Biogeografické členění České republiky.* Enigma, Praha, 347 pp. (in Czech).

DIERßEN K. 2001: Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum Bibliotheca* **56:** 1–289.

DÜLL R. 1983: Distribution of the European and Macaronesian liverworts (Hepaticophytina). *Bryologische Beiträge* **2:** 1–115.

DÜLL R. 1984: Distribution of the European and Macaronesian mosses (Bryophytina). Part I. *Bryologische Beiträge* **4:** 1–113.

DÜLL R. 1985: Distribution of the European and Macaronesian mosses (Bryophytina). Part II. *Bryologische Beiträge* **5:** 110–232.

DURING H.J. 1979: Life strategies of Bryophytes: a preliminary review. *Lindbergia* **5:** 2–18.

DURING H.J. 1990: *Clonal growth patterns among bryophytes.* Pp. 153–176. In: GROENENDAEL J. VAN & DE KROON H.: *Clonal growth in plants: regulation and function.* SPB Academic Publishing, Hague, 196 pp.

DURING H.J. 1992: *Ecological classification of bryophytes and lichens.* Pp. 1–31. In: BATES J.W. & FARMER A.M. (eds): *Bryophytes and lichens in a changing environment.* Clarendon Press, Oxford, 404 pp.

FREY W., FRAHM J.-P., FISCHER E. & LOBIN W. 1995: *Die Moos- und Farnpflanzen Europas.* Gustav Fischer Verlag, Stuttgart, 426 pp (in German).

GIMINGHAM C.H. & BIRSE E.M. 1957: Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habitat. *Journal of Ecology* **45:** 533–545.

GONZÁLEZ-MANCEBO J.M. & HERNÁNDEZ-GARCÍA C.D. 1996: Bryophyte life strategies along an altitudinal gradient in El Canal y Los Tiles (La Palma, Canary Islands). *Journal of Bryology* **19:** 243–255.

HACHTEL M., WEDDELING K. & MÖSELER B.M. 1999: Zusammenhänge zwischen Mikroklima und Moosvegetation der Arkose-Blockhalden im Warchetal (Hohe Ardennen / Belgien). *Decheniana* **37:** 49–65 (in German).

HALFMANN J. 1991: Die Struktur der Vegetation auf periglazialen Basaltblockhalden des Hessischen Berglandes. *Dissertationes Botanicae* **168:** 1–212 (in German).

HERBEN T. 2003: *Program for the calculation of relative values of potential direct irradiation.* URL: http://botany.natur.cuni.cz/cz/studium/pot_radiace.htm (March 2003).

KUBÁT K. 1974: Proudění vzduchu sutěmi jako ekologický faktor. *Opera Corcontica* **11:** 53–62 (in Czech).

KUBEŠOVÁ S. 2000: Bryophytes in a block field microrelief: case studies from SW Moravia. *Acta Universitatis Purkynianae, Stud. Biol.* **4:** 113–125.

KUBEŠOVÁ S. 2002: Mechorosty na balvanových mořích v Národním parku Podyjí. *Thayensia* **4:** 85–89 (in Czech).

KÜRSCHNER H. 1999: Life strategies of epiphytic bryophytes in Mediterranean *Pinus* woodlands and *Platanus orientalis* alluvial forests of Turkey. *Cryptogamie, Bryologie* **20:** 17–33.

KÜRSCHNER H. & PAROLLY G. 1998: Lebensstrategien stammepiphytischer Moose in Regenwäldern am Andenostabhang um im Amazonas-Tiefland von Nord-Peru. *Nova Hedwigia* **67:** 1–22 (in German).

KÜRSCHNER H., TONGUÇ Ö. & YAYINTAŞ A. 1998: Life strategies in epiphytic bryophyte communities of the southwest Anatolian *Liquidambar orientalis* forests. *Nova Hedwigia* **66:** 435–450.

LARSON D.W., SPRING S.H., MATTHES-SEARS U. & BARTLETT R.M. 1989: Organization of the Niagara Escarpment cliff community. *Canadian Journal of Botany* **67:** 2731–2742.

LÜTH M. 1999: Moosgesellschaften und Moosgesellschaftskomplexe auf Blockhalden. *Decheniana* **37:** 93–100 (in German).

MÄGDEFRAU K. 1982: *Life-forms of Bryophytes.* Pp. 45–58. In: SMITH A.J.E. (ed.): *Bryophyte Ecology.* Chapman & Hall, London, 511 pp.

MATĚJOVSKÁ O. (ed.) 1991: *Geologic map of the Czech Republic 1:50 000. 24–33 Moravský Krumlov.* Český geologický ústav, Praha (in Czech).

MOLENDA R. 1999: Die Rolle von Blockhalden bei der Entstehung disjunkter Areale: zoogeographische Aspekte. *Decheniana* **37:** 163–170 (in German).

MÖSELER B.M. & WUNDER J. 1999: Kaltluftströme auf Blockhalden und ihre Auswirkungen auf Flora und Vegetation. *Decheniana* **37:** 43–47 (in German).

NĚMCOVÁ L. 2000: Die Moose auf den Blockhalden des Böhmischen Mittelgebirges und der benachbarten Gebiete. Eine erste Skizze. *Acta Universitatis Purkynianae, Stud. Biol.* **4:** 97–111.

NĚMCOVÁ L. 2001: *Mechorosty a jejich společenstva na sutích v Českém středohoří a sousedních územích.* Manuscript, Ph.D. thesis. Deposited at Charles University, Praha (in Czech).

ORBÁN S. 1989: *The coenological and ecological connections of the life strategies of bryophytes.* Pp. 172–179. In: HERBEN T. & MCQUEEN C.B. (eds): *Proceedings of the Sixth CEBWG Meeting.* Czechoslovak Academy of Sciences, Průhonice, 283 pp.

POSPÍŠIL V. 1985: Die Laubmoose *Pterigynandrum filiforme* Hedw. und *Platygyrium repens* (Brid.) B. S. G., mögliche Indikatoren der Luftverschmutzung, in der Tschechoslowakei. *Acta Musei Moraviae, Sci. Nat.* **52:** 115–145 (in German).

PUJMANOVÁ L. 1989: Mechorosty sutí na Binově a Kamenci ve Verneřickém středohoří. *Severočeskou Přírodou* **23:** 91–95 (in Czech).

PUJMANOVÁ L. 1990: Mechorosty Borče. *Severočeskou Přírodou* **24:** 91–96 (in Czech).

QUITT E. 1971: Klimatické oblasti Československa. *Studia Geographica* **16:** 1–79 (in Czech).

QUITT E. 1975: *Mapa klimatických oblastí ČSR 1:500 000.* Geografický ústav ČSAV, Brno, 73 pp (in Czech).

Sádlo J. & Kolbek J. 1994: Náčrt nelesní vegetace sutí kolinního až montánního stupně České republiky. *Preslia* **66:** 217–236 (in Czech).

Schofield W.B. 1981: Ecological significance of morphological characters in the moss gametophyte. *The Bryologist* **84:** 149–165.

Skalický V. 1988: *Regionálně fytogeografické členění.* Pp. 103–121. In: Hejný S. & Slavík B. (eds): *Květena České socialistické republiky. 1.* Academia, Praha, 557 pp (in Czech).

Smith A.J.E. 1982: *Epiphytes and epiliths.* Pp. 191–225. In: Smith A.J.E. (ed.): *Bryophyte ecology.* Chapman & Hall, London, 511 pp.

ter Braak C.J. & Šmilauer P. 1998: *CANOCO, version 4.* Centre for Biometry, Wageningen.

Weddeling K. & Hachtel M. 2000: Struktur und kleinstandörtliche Verteilung von Moosgesellschaften auf Arkose-Blockhalden im Warchetal / Ardennen. *Acta Universitatis Purkynianae, Stud. Biol.* **4:** 73–95 (in German).

Wunder J. & Möseler B.M. 1996: Kaltluftströme auf Basaltblockhalden und ihre Auswirkung auf Mikroklima und Vegetation. *Flora* **191:** 335–344 (in German).

APPENDIX

List of recorded species, their growth-forms, life-strategies and chorological types

Growth-forms: D – dendroid, LC – large cushion, OT – open turf, RM – rough mat, SC – small cushion, SM – smooth mat, ST – short turf, T – tail, TT – tall turf, W– weft.

Life-strategies: C – colonists, CP – pioneer colonists, D – dominant, F – fugitives, L – long-lived shuttle, S – short-lived shuttle, P – perennials, PC – competitive perennials, PS – stress-tolerant perennials.

Amblystegium serpens . . . . . RM, P, temperate
Anomodon attenuatus . . . . . W, P, subcontinental-(montane)
Antitrichia curtipendula . . . . . RM, L, suboceanic
Atrichum undulatum . . . . . TT, S, temperate
Aulacomnium androgynum . . . . . ST, C, temperate
Barbilophozia barbata . . . . . RM, PS, sub-boreal-montane
Barbilophozia hatcheri . . . . . RM, CP, boreal-montane
Bartramia pomiformis . . . . . LC, L, boreal-(montane)
Bazzania trilobata . . . . . RM, PC, sub-boreal
Brachythecium glareosum . . . . . RM, PC, sub-boreal-(montane)
Brachythecium populeum . . . . . RM, P, temperate
Brachythecium reflexum . . . . . RM, PS, suboceanic
Brachythecium rutabulum . . . . . RM, CP, temperate
Brachythecium salebrosum . . . . . RM, CP, sub-boreal
Brachythecium velutinum . . . . . RM, P, temperate
Bryum capillare . . . . . ST, C, temperate
Bryum subelegans . . . . . ST, C, -
Buxbaumia aphylla . . . . . OT, F, boreal
Cephaloziella divaricata . . . . . ST, C, temperate
Ceratodon purpureus . . . . . ST, C, temperate
Cynodontium polycarpon . . . . . ST, C, boreal-montane
Dicranella heteromalla . . . . . ST, C, temperate
Dicranodontium denudatum . . . . . TT, PC, boreal-montane
Dicranum fulvum . . . . . TT, C, temperate-montane
Orthodicranum montanum . . . . . ST, PC, sub-boreal
Dicranum polysetum . . . . . TT, PC, boreal
Dicranum scoparium . . . . . LC, PC, sub-boreal
Eurhynchium angustirete . . . . . W, P, subcontinental
Eurhynchium hians . . . . . W, CP, temperate
Eurhynchium schleicheri . . . . . W, P, submediterranean-suboceanic
Frullania dilatata . . . . . SM, L, temperate
Grimmia ovalis . . . . . SC, C, sub-boreal-montane
Grimmia trichophylla . . . . . SC, PC, temperate-(montane)

Hedwigia ciliata . . . . . T, L, sub-boreal-(montane)
Homalia trichomanoides . . . . . W, PS, temperate
Homalothecium sericeum . . . . . RM, P, temperate
Hylocomium splendens . . . . . W, PC, sub-boreal
Hypnum cupressiforme . . . . . RM, PS, temperate
Pseudotaxiphyllum elegans . . . . . RM, CP, suboceanic
Isothecium alopecuroides . . . . . D, PS, temperate
Jamesoniella autumnalis . . . . . RM, C, sub-boreal-montane
Lejeunea cavifolia . . . . . SM, L, suboceanic-montane
Leskea polycarpa . . . . . RM, P, temperate
Leucodon sciuroides . . . . . T, L, temperate
Lophocolea bidentata . . . . . W, PC, temperate
Lophocolea heterophylla . . . . . RM, CP, temperate
Lophocolea minor . . . . . RM, C, temperate
Lophozia excisa . . . . . RM, CP, boreal-montane
Lophozia longidens . . . . . RM, C, boreal-montane
Lophozia ventricosa . . . . . RM, CP, boreal
Metzgeria furcata . . . . . TM, P, temperate
Mnium spinulosum . . . . . ST, L, subcontinental-montane
Orthotrichum affine . . . . . SC, C, temperate
Orthotrichum anomalum . . . . . SC, C, temperate
Paraleucobryum longifolium . . . . . LC, P, boreal-montane
Plagiochila asplenioides . . . . . RM, P, temperate
Plagiochila porelloides . . . . . RM, PS, sub-boreal-montane
Plagiomnium affine . . . . . RM, PC, temperate
Plagiomnium cuspidatum . . . . . RM, PC, sub-boreal
Plagiomnium undulatum . . . . . W, PC, temperate
Plagiothecium cavifolium . . . . . RM, PS, boreal-(montane)
Plagiothecium denticulatum . . . . . RM, PC, sub-boreal
Plagiothecium laetum (*P. laetum* s.str. was not recorded, all records are *P. curvifolium*) . . . . . RM, PS, boreal
Plagiothecium succulentum . . . . . RM, PC, suboceanic
Platygyrium repens . . . . . RM, PS, subcontinental
Pleurozium schreberi . . . . . W, PC, sub-boreal
Pohlia cruda . . . . . ST, CP, temperate-montane
Pohlia nutans . . . . . ST, CP, sub-boreal
Polytrichum cf. *longisetum* . . . . . TT, PC, boreal
Polytrichum commune . . . . . TT, PC, sub-boreal
Polytrichum formosum . . . . . TT, PC, temperate
Polytrichum juniperinum . . . . . TT, PS, temperate
Polytrichum piliferum . . . . . TT, PS, temperate
Porella platyphylla . . . . . RM, PS, temperate
Pterigynandrum filiforme . . . . . RM, PS, boreal-montane

Ptilidium ciliare . . . . . RM, L, boreal
Ptilidium pulcherrimum . . . . . RM, S, boreal
Racomitrium lanuginosum . . . . . TT, PS & D, boreal-montane
Racomitrium microcarpon . . . . . TT, CP, boreal-montane
Radula complanata . . . . . SM, L, temperate
Rhabdoweisia fugax . . . . . LC, C, boreal-montane
Rhynchostegium confertum . . . . . RM, P, sub-Mediterranean-oceanic
Rhytidiadelphus triquetrus . . . . . W, PC, sub-boreal
Schistidium apocarpum . . . . . SC, CP, temperate
Tetraphis pellucida . . . . . ST, CP, temperate
Thuidium recognitum . . . . . W, PS, suboceanic-montane
Thuidium tamariscinum . . . . . W, P, suboceanic
Tortula ruralis . . . . . ST, C, temperate