OIKOS 109: 323–330, 2005

Bryophyte colonisation in experimental microcosms: the role of nutrients, defoliation and vascular vegetation

E. Aude and R. Ejrnæs

Aude, E. and Ejrnæs, R. 2005. Bryophyte colonisation in experimental microcosms: the role of nutrients, defoliation and vascular vegetation. – Oikos 109: 323–330.

A three-year multi-factorial microcosm experiment simulating fertilisation, defoliation and the composition of vascular vegetation in a dry grassland succession was used to test four hypotheses concerning the establishment and survival of bryophytes in grassland vegetation. H_1: bryophyte cover may be used to predict bryophyte species richness. H_2: bryophyte richness is suppressed at high nutrient levels and promoted by defoliation of vascular plants. H_3: species richness of bryophytes is influenced by the species composition of the vascular vegetation. H_4: bryophyte species richness is negatively correlated with vascular plant biomass.

The relationship between bryophyte richness and bryophyte cover was found to follow the classical species-area richness curve. Bryophyte species richness responded positively to defoliation and negatively to fertilisation. The species composition of vascular vegetation had no significant effect on bryophyte richness. Bryophyte species richness was lower at high vascular plant biomass and vascular plant dry weight above 400 g m^{-2} appeared fatal to bryophytes. At high nutrient levels, defoliation increased bryophyte richness, but defoliation did not fully compensate for the negative effect of fertilisation. The study reinforces the concern for short lived shuttle bryophytes in the agricultural landscape.

E. Aude and R. Ejrnæs, Dept of Wildlife Ecology and Biodiversity, National Environmental Research Institute, Grenåvej 12, DK-8410 Rønde, Denmark. Present address for EA: HabitatVision, Askedalsvej 3, DK-8410 Rønde, Denmark (eau@habitatvision.dk). Present address for RE: Arctic Station, Univ. of Copenhagen, 3953 Qeqertarsuaq, Greenland.

Bryophytes are claimed to be good indicators of habitat quality and of the ecological function of habitats (Carroll et al. 2000, Hylander et al. 2002). The lack of sclerenchyma makes bryophytes vulnerable to competitive exclusion by vascular plants and potentially suitable as early indicators of environmental change. Moreover, most bryophytes are poikilohydric and ectohydric, taking up water and nutrients over their entire surface, and therefore particular sensitive to e.g. climatic fluctuations (Økland 1995). A few sporadic repeated surveys in European dry grassland have documented marked changes in the bryophyte flora, especially in areas with an intensive agricultural sector such as Holland and Denmark (During and Willems 1986, Ejrnæs and Poulsen 2001). On the other hand, only minor changes have been found in more protected chalk grassland areas in Britain (Porley 1999).

Nutrient availability (or fertility) is one of the most studied factors in vegetation science and it is generally accepted that high nutrient levels increases competitive asymmetry and thereby influences the composition and richness of vascular vegetation in different community types (Milton and Davies 1947, Grime 1979, Bobbink 1991, Keddy et al. 1997, Kleijn et al. 1997). Nutrient experiments have only incidentally considered changes in the bryophyte flora, with Willis (1963), Bobbink (1991) and Virtanen et al. (2000) as exceptions. Some bryophytes have been reported to compete successfully with

Accepted 8 November 2004

ISSN 0030-1299

seedlings and small vascular plants (Rydin 1997) and some can attain growth rates higher than many vascular plants and thereby coexist with even very productive vascular plants (Furness and Grime 1982). However, while some bryophyte species respond to nutrients (Stjernquist 1981, Li and Vitt 1994) other bryophytes hardly show any response (Skre and Oechel 1979, Dirkse and Martakis 1992). Indeed, both field observations (Richards 1928, Jeffrey and Pigott 1973, Bergamini et al. 2001) and experiments (Mickiewicz 1976, Lambert et al. 1986, Virtanen et al. 2000) point in the direction of a suppression of bryophytes with increasing vascular plant biomass. On the other hand, not all studies find changes in the balance between the two plant groups as a result of eutrophication of grassland (Bobbink 1991, Carroll et al. 2000). Almost 50 years ago, Watson (1960) put forward the idea that not only the biomass, but also the species composition of vascular vegetation in grassland influenced the bryophyte performance. To our knowledge this hypothesis remains untested.

Grazing and mowing intensity are known to influence the performance of vascular species (Godwin 1941, Rieley and Page 1990) and bryophytes (Richards 1928, Lambert et al. 1986, Virtanen et al. 2000). However, one study from moist grassland showed no effect of grazing intensity and hay making on the cover and diversity of bryophytes (Quene and Bakker 1988).

Only a few experimental studies have investigated the combined effects of mowing and nutrient addition on vascular plants and bryophytes (Bergamini and Peintinger 2002). In their short-term field experiment, Bergamini and Peintinger (2002) found only a minor effect of defoliation and hardly any effect of eutrophication.

The variety of studies and results leave a number of untested hypotheses regarding the mechanisms of colonisation and survival of bryophytes in grasslands.

In this study we investigated the effects of nutrient level and defoliation, alone and in combination, on bryophyte richness in grassland. We also revisited the idea of Watson (1960) that species composition of vascular vegetation affects bryophyte richness. Finally we analysed the relationship between bryophyte cover and bryophyte richness, based on the hypothesis that increased bryophyte abundance may be a result of clonal growth of typical one species.

There has been a steady increase in the use of microcosms in experimental community ecology over the last decades, and due to ease of replication and manipulation, microcosms have proven a very successful approach to formal testing of hypotheses regarding complex ecological mechanisms and relationships (Fraser and Keddy 1997).

The objective of this study is thus to test the following four hypotheses by use of experimental microcosms:

H_1: bryophyte cover may be used to predict bryophyte species richness in grassland.

H_2: bryophyte richness is suppressed at high-nutrient level and promoted by defoliation of vascular plants. The effect of defoliation depends on nutrient status and vice versa.

H_3: species richness of bryophytes is influenced by the species composition of the vascular plants.

H_4: bryophyte species richness is negatively related to vascular plant biomass.

Methods

In May 1998 a three-year multi-factorial outdoor experiment using $0.37 \times 0.27 \times 0.28$ m plastic boxes was established on a research field at the National Environmental Research Institute, at Kalø, Denmark. The average temperature for January and July is 0.2 and 16.2°C, respectively, and the mean annual precipitation is 642 mm (Frich et al. 1997, Laursen et al. 1999).

The microcosms were placed 25 m north of a forest edge on a 30 cm sand layer covering a well drained former agricultural field. The growth medium consisted of a per volume mixture of ¾ gravel pit sand and ¼ dried peat, having a pH of 7.2. A mixed inoculum composed of soil water extract and finely chopped grass roots from old calcareous dry grassland (Strands), acidic grassland (Trehøje) and a productive road verge vegetation (Kalø) was added to the growth medium to provide potentially important microorganisms (e.g. mycorrhiza, microfungi and bacteria species) and bryophyte spores. All microcosms received the same initial standardised inoculum and were thereafter left to spontaneous colonisation.

To avoid severe droughts, microcosms were watered during long dry periods in June–August. Three treatments, each with two levels, were applied to the microcosms: (1) fertilised (+F) vs unfertilised (−F), (2) cut (+C) vs uncut (−C), (3) composition of vascular plant vegetation: generalist (G) vs specialist (S) species. The eight different treatment combinations were replicated four times. Unfortunately we had to exclude one of the microcosms due to unintended disturbance, which left us with 31 microcosms.

In the first year, when microcosms were established, nutrients were applied as commercial liquid fertiliser (complete with micronutrients). +F microcosms received three monthly additions from May to July, in total 16.5 g N, 2.7 g P and 13 g K m^{-2}. −F microcosms received only one application, in June, corresponding to 0.37 g N, 0.06 g P and 0.29 g K m^{-2}. In subsequent years, an annual application was given in the form of solid NPK granulate including micronutrients to +F microcosms only, corresponding to 12.6 g N, 2.7 g P and 16 g K m^{-2}

Grazing was simulated by cutting the vegetation to 40 mm every month from May to October, with removal of

the cut material from the microcosms. A common pool of 48 vascular plant species were introduced in the microcosms (30 seeds each), of which 24 species were selected a priori to represent generalist grassland species (e.g. *Lolium perenne*, *Dactylis glomerata* and *Plantago lanceolata*) and 24 species to represent seminatural grassland specialists (e.g. *Festuca ovina*, *Avenula pratensis* and *Geranium sanguineum*). Each species subset included equal proportions of annuals and perennials as well as grasses and forbs. In 50% of the microcosms, specialist species were sown in the first year and generalist species in the second year, and vice versa in the other half. Appendix 1 reports the surviving vascular plant species in each of the eight combinations of treatments. The composition of vascular plants was therefore an emergent property of the sequential species addition.

In October 2001, after 3½ year, all aboveground biomass of bryophytes and vascular plants was harvested from half of the area in each microcosm. In the laboratory, bryophytes were sorted into different taxa, under the stereoscope. The cover was measured by placement of each taxon on a cm-grid, recording cover to nearest cm^2. Dry weight of vascular plants was measured after drying at 80°C for 24 h. Taxonomy and nomenclature of bryophytes follow Corley et al. (1981) and Corley and Crundwell (1991) whereas vascular plants follow Flora Europaea (Tutin et al. 1964–1993). *Bryum* and *Pottia* were identified to genus only because of lack of fertile specimens.

Data analyses

Statistical analyses were selected to address directly each of the five hypotheses stated in the introduction.

H_1: we hypothesised that the cover-richness relationship followed the well-known species-area relationship that goes back to Arrhenius (1921): $S = cA^z$, where S = species number of bryophytes, A = total area (= cover) of bryophytes, and c and z are constants that vary with the studied organisms, habitat type and configuration of habitats (e.g. isolation). Under this assumption, we log-transformed richness and cover, to obtain a linear relationship of the form: $\log S = \log c + z \log A$. We excluded data from boxes without bryophytes from this analysis, as the figures for the independent and dependent variables are fixed in this case.

H_2: to test the hypothesis that high nutrient level suppresses, and defoliation promotes bryophyte diversity, we carried out an ANOVA of bryophyte richness as a function of the treatments. We included interaction terms in the ANOVA to test the sub-hypothesis that the effect of defoliation depended on nutrient level and vice-versa.

H_3: we tested the hypothesis regarding effects of species composition of vascular vegetation by an ANOVA that included the sequence treatment (that equals dominance of generalists vs specialists) of the experiment and any interaction between the sequence treatment and defoliation or nutrient level. We used type III sums of squares in calculation of variable contribution in the ANOVA-model because the exclusion of one replicate led to a slightly unbalanced experimental design.

H_4: we tested the relationship between vascular biomass and richness by linear regression, using a log-transformation of vascular biomass in order to obtain linearity.

Results

In total 17 bryophyte taxa (six pleurocarps and 11 acrocarps) were found in the 31 microcosms with an average of 4.8 taxa per microcosm. Four microcosms remained without bryophytes throughout the experimental period, and a maximum of nine species was observed in three microcosms. The most abundant acrocarp taxa were *Ceratodon purpureus* and *Bryum* sp., and the most abundant pleurocarp species were *Brachythecium rutabulum* and *Eurhyngium praelongum* (Table 1).

The microcosms varied considerably in vascular plant species composition. Dry weight of the 20 harvested vascular species, 8 generalist species and 12 specialist species, are shown in the Appendix. The minimum number of vascular species (5) was found at high nutrient levels without defoliation and with a dominance of generalist species. The maximum number of vascular species (17) was found at low nutrient levels, with defoliation and with dominance of specialist grassland species. The most species-rich microcosms were characterised by a variety of species with no clear dominant species (Appendix 1). The effect of colonisation sequence on species was clearly visible after 3 years, and no generalist species was able to obtain high biomass values in the specialist microcosms or vice versa (Appendix 1).

A log–log regression showed a highly significant positive linear relationship between log(cover) and log(richness) of bryophytes ($r^2 = 0.75$, Fig. 1), confirming H_1. The linear regression revealed a parameterised relationship: $S = 1.9 \times Cover^{0.36}$.

Bryophyte species richness was negatively affected at high-nutrient level ($r^2 = 0.69$, $P < 0.001$) and positively by defoliation (Table 2). Although the results point in the direction of an interaction between defoliation and nutrient level, the interaction term was not significant ($p = 0.08$). A more detailed investigation of the interactions showed that defoliation exerted a significant effect on richness in the high-nutrient situation (mean of cut = 5, mean of uncut = 1.25, $p = 0.003$, students

Table 1. Mean cover (cm^2) of colonising bryophyte species at different fertilisation and defoliation regimes. Species are ordered according to decreasing total cover. n: number of replicates.

	Mean cover of species				Total cover
Nurients	+F	+F	−F	−F	
Defoliation	+C	−C	+C	−C	
n	8	8	8	7	
Bryum sp.	10	0.5	64.3	33.3	864
Ceratodon purpureus	12.7	0.1	49	38.5	802
Eurhyngium praelongum	31.3	0.6	18.9	21.4	577
Pohlia nutans	11.6	0.6	20.1	4.1	292
Brachythecium rutabulum	13	5.4	11.1	6.5	289
Funaria hygrometrica	<1	–	9.8	1.3	90
Hypnum cupressiforme	<1	–	1.6	6.5	68
Rhytidiadelphus squarrosus	–	–	–	7	56
Amblystegium serpens	1.9	<1	3.1	<1	48
Brachythecium albicans	3.3	–	–	–	26
Dicranella crispa		–	<1	–	7
Barbula unguiculata	<1	–	<1	–	6
Pottia sp.	–	–	<1	–	6
Ditricum pusillum	–	–	–	<1	3
Racomitrium heterostichum	–	–	<1	–	<1
Mnium marginatum	–	–	<1	–	<1
Ditricum heteromallum	–	–	<1	–	<1

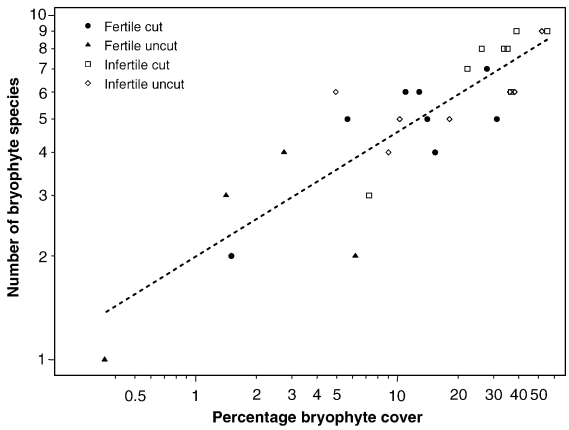

Fig. 1. Relationship between log(bryophyte cover) and log(number of bryophyte species) ($p < 0.001$). A linear regression model explained 75% of the variation ($r^2 = 0.75$).

T-test), while the effect within the low-nutrient situation was non-significant (mean of cut = 7.25, mean of uncut = 5.86, $p = 0.16$). The first half of hypothesis H_2 is thus confirmed, while the second part is less clear.

Species composition of vascular vegetation exerted no measurable effect on bryophyte richness (Table 2). We therefore had to reject hypothesis H_3. On the other hand the number of bryophytes species decreased significantly as the biomass of vascular plants rose (log–log relationship, $r^2 = 0.58$, Fig. 2), confirming hypothesis H_4. Maximum bryophyte richness and occurrence of acrocarps were found below a dry weight of vascular plants of 200 g m^{-2}, whereas a dry weight above 400 g m^{-2} appeared fatal to bryophytes (Fig. 2, Table 1).

Discussion

Cover-richness relationships of bryophytes

The successful application of the species–area relationship known from macroecology to the microcosm situation in this study is new to our knowledge. Berglund and Jonsson (2001) studied area–richness relationships for six different taxonomic groups in fragments of old-growth boreal forests. They found z-values ranging from

Table 2. ANOVA (type III sum of squares) comparing the mean number of bryophyte species at different treatments. ($r^2 = 0.69$). Residual standard error = 1.78.

Treatment	Mean number of bryophyte species in the three treatments	Sums of squares	Probability
Fertilisation	−F = 6.6 +F = 3.1	89.653	0.000021
Sequence	specialists = 5.0 generalists = 4.6	0.853	0.61
Defoliation	+C = 6.1 −U = 3.4	51.253	0.00052
Fertilisation × sequence		0.053	0.9
Fertilisation × defoliation		10.453	0.08
Sequence × defoliation		0.853	0.6
Fertilisation × sequence × defoliation		1.333	0.5

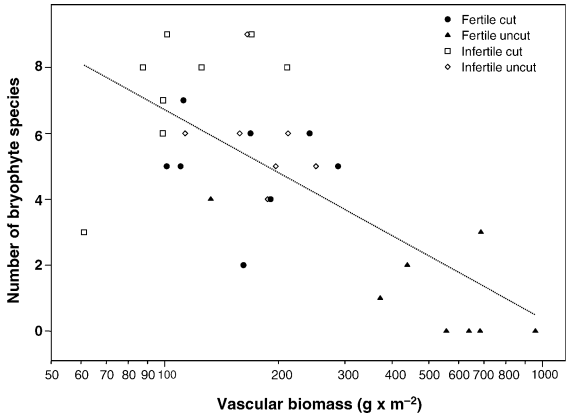

Fig. 2. Relationship between log(biomass of vascular plants) and number of bryophyte species ($p < 0.001$). A linear regression model explained 58% of the variation ($r^2 = 0.58$).

0.1 to 0.41 with a mean of 0.23 and c values ranging from 13 to 25 with a mean of 20. While our z-value of 0.36 is within this range our c-value is much lower, but not surprisingly so as our study is in micro-scale, constraining c to be a small number. Compared to our r^2 of 0.75, the values in Berglund and Jonsson (2001) were much lower (0.49 to 0.70) probably reflecting field conditions with more covarying environmental factors. On the other hand the classical use of A is a fixed area (Gitay et al. 1991), instead we used the total cover of bryophyte "island" inside the grassland as area and thereby excluding empty spaces leading to higher z-values. Furthermore others have likewise found that the Arrhenius relationship runs into problems once the areas become too small (Williamson et al. 2001).

Positive relationships between cover and richness of bryophytes have previously been reported along an elevation gradient (Slack 1977), in boreal spruce forest (Økland 1994) and significant relationship between bryophyte abundance and species number were also found in fen vegetation (Bergamini et al. 2001). Further, highest species richness of bryophytes coincided with maximum bryophyte biomass in the long-term grassland field experiment of Virtanen et al. (2000), but the relationship was not significant. Our result suggests that bryophyte cover may be considered as an indicator of habitat quality for bryophytes and possibly also lichens in grassland monitoring.

Bryophytes and coexistence with vascular plants

Our results show that species richness of bryophytes decreased at high nutrient level and increased when biomass is removed by defoliation. The interpretation of vascular plant biomass as an important cause for the variation in bryophyte richness is supported by the significant decrease in richness along the biomass gradient. We suggest that the reported relationship corresponds to the upper end of the humped-back relationship between biomass and species richness of vascular plants (Al-Mufti et al. 1977) – except that the optimum is shifted towards lower biomass values for bryophyte richness. It is worth noticing however that vascular biomass explained less variation in bryophyte richness than did the experimental treatments. One possible explanation, which is supported by the stronger relationship to bryophyte cover (Fig. 1) is that the low biomass observed in defoliated and high-nutrient microcosms poorly reflects the competition for the two dimensional space in the dense sward.

The observed suppression of bryophytes following high-nutrient level is in accordance with the majority of grassland field observations (Richards 1928, During 1992) and grassland field experiments (Willis 1963, Jeffrey and Pigott 1973, Mickiewicz 1976, Carroll et al. 2000, Virtanen et al. 2000) and similar results have been reported from heathland and wetland vegetation (Berendse et al. 2001, Bergamini et al. 2001). However, not all studies of bryophytes point in this direction. Bergamini and Peintinger (2002) studied vegetation in a fen and found a seven-fold increase in photon flux density after vascular plant removal, but no biomass increase in bryophytes. Moreover they found no effects of fertiliser application on the growth of one transplanted bryophyte species. The short duration of their experiment (3 months) or almost fully cover of bryophytes may however explain the absence of bryophyte response. Morecroft et al. (1994) studied two grassland types, and apart from a reduction in *Rhytidiadelphus squarrosus* almost no differences in bryophyte species composition was found as a result of increasing ammonium nitrate input for three years. This result was not completely surprising and is probably caused by a considerable response delay time (inertia sensu Milchunas and Lauenroth 1995) once the vegetation has been established. This emphasises the limited relevance of short-lasting experiments in established vegetation.

The notion that biomass removal in the form of grazing or mowing is important for bryophytes in grassland has a long history (Richards 1928). Nevertheless, only a few studies have studied nutrient level and defoliation in combination (Bergamini and Peintinger 2002). It was unexpected that the interaction between defoliation and nutrient level was not significant ($P = 0.08$), but this should be interpreted in the light of the low number of replicates ($n = 4$). Our results also demonstrated that although defoliation and biomass removal may prevent bryophyte extinction, grazing is not a sufficient management measure for preserving bryophyte diversity in grasslands with high nutrient inputs. On the contrary, defoliation at high nutrient levels resulted in significant lower cover and fewer species of bryophytes than low nutrient levels without

defoliation. Five out of 11 acrocarp bryophytes were unable to colonise and survive at high nutrient levels even with biomass removal. This emphasises the current threats to especially acrocarp bryophytes (Longton 1992).

Species composition of vascular plants

Although it has been suggested that different vascular plants, e.g. *Dactylis glomerata*, were inimical to bryophytes (Watson 1960), our results showed that it is the productivity and thereby the structural properties of the vegetation in combination with the disturbance regime that determine bryophyte cover and richness in grassland vegetation. On the other hand, the environmental condition obviously has a decisive role for species composition of vascular vegetation under unmanipulated field conditions – and hereby we are offered an obvious explanation for the patterns observed by Watson (1960).

Observed changes in the bryophyte flora of dry grassland in Europe

Our findings reinforce the concerns stated by During and Willems (1986) and During (1992) that eutrophication leads to a decrease of pioneers and short-lived shuttle bryophytes and a concomitant increase of competitive perennial bryophytes. Ejrnæs and Poulsen (2001) hypothesised that increased abundance of *Brachythecium rutabulum* and *Ceratodon purpureus* in dry grasslands could be caused by increased abundance of these highly dispersive and persistent species in the surrounding agricultural landscape. Our study supports the notion of a consistent negative effect of eutrophication on bryophyte species richness and further supports the notion of *B. rutabulum* as an effective coloniser showing remarkable survival capacity in productive vegetation with high vascular plant biomass.

Perspectives

In intensive agricultural landscapes the nutrient levels can be even higher than those imposed in our experiment. Hedgerows, road verges, field margins and similar small biotopes embedded in cultivated land (Agger and Brandt 1988) accumulate nutrients from fertiliser application to neighbouring fields and also from atmospheric deposition of nitrogen. As a result of this, the network of uncultivated biotopes in the agricultural landscape lose their function as dispersal corridors and habitat refuges for bryophytes (and stress-tolerant vascular plants). The longterm perspective is a landscape with tiny islands of infertile grasslands surrounded by highly productive vegetation, where highly dispersive and shade-tolerant bryophytes will increase at the expense of the majority of more stress-tolerant bryophytes.

Acknowledgements – Sincere thanks to Annie Laursen, Bettina Nygaard, Håkan Rydin, Simon Lægård, Rune Økland and J. Bastow Wilson for improving earlier versions of this paper.

References

Agger, P. and Brandt, B. J. 1988. Dynamics of small biotopes in Danish agricultural landscapes. – Landscape Ecol. 1: 227–240.

Al-Mufti, M. M., Sydes, C. L., Furness, S. B. et al. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. – J. Ecol. 65: 759–791.

Arrhenius, O. 1921. Species and area. – J. Ecol. 9: 95–99.

Berendse, F., Van Breemen, N., Rydin, H. et al. 2001. Raised atmospheric CO2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. – Global Change Biol. 7: 591–598.

Bergamini, A. and Peintinger, M. 2002. Effects of light and nitrogen on morphological plasticity of the moss *Calliergonella cuspidata*. – Oikos 96: 355–363.

Bergamini, A., Pauli, D., Peintinger, M. et al. 2001. Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. – J. Ecol. 89: 920–929.

Berglund, H. and Jonsson, B. G. 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. – J. Veg. Sci 12: 857–866.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. – J. Appl. Ecol. 28: 28–41.

Carroll, J. A., Johnson, D., Morecroft, M. et al. 2000. The effect of longterm nitrogen addition on the bryophyte cover of upland acidic grasslands. – J. Bryol. 22: 83–89.

Corley, M. F. V. and Crundwell, A. C. 1991. Additions and amendments to the mosses of Europe and the Azores. – J. Bryol. 16: 337–356.

Corley, M. F. V., Crundwell, A. C., Düll, R. et al. 1981. Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. – J. Bryol. 11: 609–689.

Dirkse, G. M. and Martakis, G. F. P. 1992. Effects of fertilizer on bryophytes in Swedish experiments on forest fertilization. – Biol. Conserv. 59: 155–161.

During, H. J. 1992. Ecological classifications of bryophytes and lichens. – In: Bates, J. W. and Farmer, A. M. (eds), Bryophytes and lichens in a changing environment. Oxford Science Publication, pp. 1–31.

During, H. J. and Willems, J. H. 1986. The impoverishment of the bryophyte and lichen flora of the Dutch grasslands in the thirty years 1953–1983. – Biol. Conserv. 36: 143–158.

Ejrnæs, R. and Poulsen, R. S. 2001. Trends in the bryophyte and lichen flora of Danish semi-natural grasslands over the last 50 years. – Lindbergia 26: 115–120.

Fraser, L. H. and Keddy, P. 1997. The role of experimental microcosms in ecological research. – Trends Ecol. Evol. 12: 478–481.

Frich, P., Rosenørn, S., Madsen, H. et al. 1997. Observed precipitation in Denmark 1961–90. Tech. Rep. 97–8. – Danish Meteorol. Inst., Copenhagen.

Furness, S. B. and Grime, J. P. 1982. Growth rate and temperature responses in bryophytes: I. An investigation of *Brachythecium rutabulum*. – J. Ecol. 70: 513–523.

Gitay, H., Roxburgh, S., Stephen, H. et al. 1991. Species-area relations in a New Zealand tussock grassland, with implications for nature reserve design and for community structure. – J. Veg. Sci. 2: 113–118.

Godwin, H. 1941. Studies in the ecology of Wicken Fen: IV. crop-taking experiments. – J. Ecol. 29: 83–106.

Grime, J. P. 1979. Plant strategies & vegetation processes. – John Wiley and Sons.
Hylander, K., Jonsson, B. G. and Nilsson, C. 2002. Evaluating buffer strips along boreal streams using bryophytes as indicators. – Ecol. Appl. 12: 797–806.
Jeffrey, D. W. and Pigott, C. D. 1973. The response of grasslands on sugar-limestone in Teesdale to application of phosphorus and nitrogen. – J. Ecol. 61: 85–92.
Keddy, P., Twolan-Strutt, L. and Shipley, B. 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. – Oikos 80: 253–256.
Kleijn, D., Joenje, W. and Kropff, M. J. 1997. Patterns in species composition of arable field boundary vegetation. – Acta Bot. Neerl. 46: 175–192.
Lambert, M. G., Clark, D. A., Grant, D. A. et al. 1986. Influence of fertiliser and grazing management on North Island moist hill country. 4. Pasture species abundance. – N. Z. J. Agr. Res. 29: 23–31.
Laursen, E. V., Thomsen, R. S. and Cappelen, J. 1999. Observed air temperature, humidity, pressure, cloud cover and weather in Denmark-with climatological standard normal, 1961–90. Tech. Rep. 99–5. – Danish Meteorol. Inst., Copenhagen.
Li, Y. H. and Vitt, D. H. 1994. The dynamics of moss establishment-temporal responses to nutrient gradients. – Bryologist 97: 357–364.
Longton, R. E. 1992. Reproduction and rarity in British mosses. – Biol. Conserv. 59: 89–98.
Mickiewicz, J. 1976. Influence of mineral fertilization on the biomass of moss. – Pol. Ecol. Stud. 2: 57–62.
Milchunas, D. G. and Lauenroth, W. K. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. – Ecol. Appl. 5: 452–458.
Milton, W. E. J. and Davies, R. O. 1947. The yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. – J. Ecol. 35: 65–95.
Morecroft, M. D., Sellers, E. K. and Lee, J. A. 1994. An experimental investigation into the effects of atmospheric nitrogen deposition on two semi-natural grasslands. – J. Ecol. 82: 475–483.
Økland, R. H. 1994. Patterns of bryopyte association at different scales in a Norwegian boreal spruce forest. – J. Veg. Sci. 5: 127–138.
Økland, R. H. 1995. Changes in the ocurrence and abundance of plant species in a Norwegian boreal coniferous forest, 1988–1993. – Nord. J. Bot. 15: 415–438.
Porley, R. D. 1999. Bryophytes of chalk grassland in the Chiltern Hills, England. – J. Bryol. 21: 55–66.
Quene, E. and Bakker, J. P. 1988. Effects of nature management-practices on the bryophyte flora of grassland and heathland in Drenthe, the Netherlands. – Acta Bot. Neerl. 37: 203–213.
Richards, P. W. M. 1928. Ecological notes on the bryophytes of Middlesex. – J. Ecol. 16: 267–300.
Rieley, J. O. and Page, S. E. 1990. Ecology of plant communities. – Longman Scientific and Technical.
Rydin, H. 1997. Competition among bryophytes. – Adv. Bryol. 6: 135–168.
Skre, O. and Oechel, W. C. 1979. Moss production in a black spruce *Picea mariana* forest with permafrost near Fairbanks, Alaska, as compared with two permafrost-free stands. – Holarct. Ecol. 2: 249–254.
Slack, N. G. 1977. Species diversity and community structure in bryophytes. New State Studies. – The Univ. of the State of New York, New York.
Stjernquist, I. 1981. Photosynthesis, growth and competitive ability of some coniferous forest mosses and the influence of herbicides and heavy metals (Cu, Zn). – PhD thesis. Dept. of Plant Ecology, Univ. of Lund, Sweden.
Tutin, T.G. et al. 1964–1993. Flora Europaea. Vol. 1–5 and Vol. 1, 2nd ed. – Cambridge Univ. Press.
Virtanen, R., Johnston, A. E., Crawley, M. J. et al. 2000. Bryophyte biomass and species richness on the Park Grass Experiment, Rothamsted, UK. – Plant Ecol. 151: 129–141.
Watson, E. V. 1960. A quantitative study of the bryophytes of chalk grassland. – J. Ecol. 48: 397–414.
Williamson, M., Gaston, L. J. and Lonsdale, W. M. 2001. The species-area relationship does not have an asymptote! – J. Biogeogr. 28: 827–830.
Willis, A. J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. – J. Ecol. 51: 353–374.

Appendix 1. Average dry weight (g) and species richness of recorded vascular vascular species in the microcosm with different treatments. G = generalist species, S = specialist species, n = number of replicates. <1 indicates dry weights below 1 g.

Nutrient level		high	high	low	low	high	high	low	low
Defoliation		uncut	cut	uncut	cut	uncut	cut	uncut	cut
Sequence		G	G	G	G	S	S	S	S
n		4	4	3	4	4	4	4	4
Rumex acetosa	G	<1	<1	3.0	1.1		<1		
Plantago lanceolata	G	3.1	2.9		1.2		<1		<1
Dactylis glomerata	G	16.0	2.9	1.0	<1				<1
Elymus repens	G	<1							<1
Festuca rubra	G	22.0	3.2	4.4	1.1				
Lolium perenne	G		<1						<1
Trifolium repens	G				1.0				
Medicago lupulina	G				2.4				2.0
Geranium sanguineum	S		<1	<1	<1		<1	<1	<1
Ranunculus bulbosus	S		<1			<1	<1	<1	<1
Lotus corniculatus	S		<1		2.3				<1
Bromus erectus	S		<1			<1		2.9	<1
Trifolium pratense	S		<1		1.0	<1	1.0		<1
Centaurea scabiosa	S					<1		1.9	<1
Galium verum	S					1.2	<1	<1	<1
Festuca ovina	S				<1	25.7	5.6	<1	<1
Agrostis capillaris	S			<1		2.8	1.3	3.3	2.0
Filipendula vulgaris	S					<1	<1	0.7	<1
Hieracium pilosella	S					<1	<1	<1	<1
Taraxacum sect Erythrospermum	S						<1	1.7	<1
Number of vascular species		5	10	7	10	9	11	10	17
Average dry weight of all vascular plants (g)		42.0	10.2	11.1	10.7	31.6	9.5	10.8	7.9