



# The bryophyte layer in a calcareous grassland after a decade of contrasting mowing regimes

Alain Vanderpoorten<sup>a,\*</sup>, Louis-Marie Delescaille<sup>b</sup>, Anne-Laure Jacquemart<sup>a</sup>

<sup>a</sup>Université Catholique de Louvain, Unité d'Ecologie & Biogéographie, 4-5 Place Croix du Sud, B-1348 Louvain-la-Neuve, Belgium

<sup>b</sup>Ministère de la Région Wallonne, Centre de recherche de la nature, des forêts et du bois, 22 avenue de la faculté d'Agronomie, B-5030 Gembloux, Belgium

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## Abstract

Analysis of variance and redundancy analysis were used to study the effects of mowing regime and herb canopy structure on the bryophyte layer of a calcareous grassland in southern Belgium. Species richness in mown and control plots did not significantly differ. In control plots, a number of grassland species were able to survive within a grassy-shrubby fringe 15 years after shrub cutting. This suggests that there might be a time-lag of at least 20 years before cessation of mowing results in a significant decrease in species number per m<sup>2</sup>. Mown plots were mostly characterized by the almost complete cover of large pleurocarps. Mowing resulted in almost continuous herb and moss layers that were unfavourable for a number of annual bryophytes, many of which are of high conservation interest. It is suggested that grazing, which increases the number of species, especially the number of pioneers, is likely to be more beneficial to bryophytes.

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## 1. Introduction

Calcareous grasslands represent a man-made, semi-natural vegetation type of high biological value (Willems, 1990). In Europe, where calcareous grasslands occupy a small and still declining area since the loss of their agricultural usefulness in many countries in the middle of the 20<sup>th</sup> century, about 700 plant species occur in this vegetation type, and roughly a third of them are restricted to this habitat (Willems, 1982). Owing to their biological richness, a number of calcareous grasslands were set aside as nature reserves that have to be actively managed to prevent a natural succession to woodland.

The conservation of biological diversity in calcareous grasslands requires an integrated approach covering the ecological demands of a multitude of organisms. In practice, however, the emphasis is often placed on the vascular flora. As a consequence, ecological management has been much more successful for the vascular flora than for a number of other taxa (WallisDeVries et al., 2002).

There are about 200 bryophyte and lichen species known from European calcareous grasslands (Willems, 1982), including a number of rare species restricted to this habitat (e.g. During et al., 1986; Odé and During, 1987; Werner, 1990; Porley, 1999), but they are seldom considered in conservation and restoration programmes (During, 1990). The extent to which management practices involved in such programmes affect the bryophyte layer is still largely unknown. Indeed, although bryophyte species composition has been investigated in relation to grassland type (Cornish, 1954; Watson, 1960), very few studies have explicitly focused on the effects of different management practices on the bryoflora. During (1990), in a review on the bryophytes of calcareous grasslands, cited only one study on the effects of grazing (Morton, 1977), while van Tooren et al. (1990, 1991) compared the species composition of different grasslands after 2 years of various management experiments including grazing and mowing at different seasons and different intensities. In this paper, we investigate how the bryophyte layer is influenced by mowing regime and vegetation structure in several plots of a calcareous grassland mown at different seasons since 1988.

\* Corresponding author.

E-mail address: [vanderpoorten@ecol.ucl.ac.be](mailto:vanderpoorten@ecol.ucl.ac.be)  
(A. Vanderpoorten).

## 2. Methods

### 2.1. Study site and experimental design

The study site consists of a calcareous grassland currently protected and managed as a nature reserve in Nismes (southern Belgium), on the flat top of a hill of hard Devonian limestone, at an altitude of about 225 m. Ancient maps of Ferraris (around 1770) and Vander Maelen (1850) reveal that the site was covered by grasslands since at least the 18th century. On an aerial photograph taken in 1935, the site appears as a complex of calcareous grasslands. Sheep grazing was progressively stopped, but a number of grasslands remained opened thanks to grazing by dense populations of rabbits.

In 1988–1989, a 175×50 m glade surrounded by oak (*Quercus robur*) woods and pine (*Pinus sylvestris*) plantations was designated for a survey on the effects of different mowing regimes on the vegetation. The glade consisted in a *Brachypodium pinnatum* grassland with sparse shrubs (*Prunus spinosa*) and small trees (*Quercus robur*, *Pinus sylvestris*) that were cut during the winter of 1988–1989. In this glade, six 100 m<sup>2</sup> plots were delimited within a completely homogeneous 30×80 m area with regard to topography and initial vegetation.

Individual plots were subjected to one of three treatments, each with two replicates to separate the floristic variation due to the treatment from that due to plot location. Although the small size of the study site only allowed minimal plot replication and did not permit the implementation of a design in blocks, the selection of a small area did allow us to select a very homogeneous site in order to reduce spatial heterogeneity as much as possible.

### 2.2. Mowing regime

Plots were mown once a year, either outside the main growth season for vascular plants, in March or in October, or during the growth season, in May or in July. The litter was raked from the inside to the outside of each plot to avoid the introduction of diaspores. Plots mown outside the growth season differed from those mown during the growth season by a slightly higher herb canopy, a slightly higher cover in *Brachypodium pinnatum* (34 vs 21% on average, respectively), and a higher cover in erect forbs vs rosette-bearing species. Control plots were characterized by a thick cover of *Brachypodium pinnatum* reaching, on average, 66%, and a well developed shrub (*Prunus spinosa*) layer.

### 2.3. Vegetation survey

In each 100 m<sup>2</sup> plot, 10 1-m<sup>2</sup> quadrats were studied along a 10 m long transect for practical reasons of delimitation. In each 1-m<sup>2</sup> quadrat, species cover (nomen-

clature of Sotiaux and Vanderpoorten, 2001) was recorded according to the following scale: 0.25 for individual shoots; 0.50 for two to several shoots with a cover <1%; 2.5 for cover between 1 and 4.9%; 15 for cover between 5 and 24.9%; 37.5 for cover between 25 and 49.9%; 62.5 for cover between 50 and 74.9%; 85 for cover between 75 and 94.9%; and 97.5 for cover between 95 and 100%. Although plots of 0.01 m<sup>2</sup> have been recommended for identification of the major gradients in the bryophyte layer (Økland, 1994; Zamfir et al., 1999), it has been shown that factors organising plant communities operate at different scales (Reed et al., 1993). As the objective of the present study was not to investigate small-scale relationships between the bryophyte layer and micro-ecological conditions, we considered that 1-m<sup>2</sup> quadrats were appropriate to demonstrate floristic tendencies related to differences in mowing practices.

Bryological surveys were undertaken in March and April 2002, a season during which all species, including annuals, are present and identifiable. Material of difficult taxa was systematically collected in each quadrat for subsequent microscopical examination.

Surveys of the vascular flora were performed several times between the spring and the fall of 2001 to take phenological differences into account. Information concerning the vascular vegetation included cover of the herb layer, minimum, maximum, and average height of the herb layer, and cover of each of the phanerogam species present in the grassland. In order to survey the influence of the canopy structure on the bryophyte layer, each species was assigned to one of eight growth forms based on the combined information from several classification systems (Barkman, 1988; Grime et al., 1988; Kahmen et al., 2002). Because these publications did not mention all the species encountered in our study site, the remaining species were assigned to one of these eight growth forms according to personal observations and descriptions of plant morphology by Stace (2001) and Jäger and Werner (2002) (Table 1). Total cover of each growth form in the 1-m<sup>2</sup> quadrats was then calculated by summation over the cover of each species exhibiting the growth form in question.

### 2.4. Statistical analyses

Differences in number of bryophyte species per quadrat and cover of individual species occurring in more than 5% of the quadrats submitted to an identical mowing regime were searched by two-way analysis of variance. Because the quadrats were organized in transects and thus were not independent from each other, the ten measurements made in each plot were used to compute an average value for each independent plot. The analysis included mowing regime as main factor *a* and plot replicate as nested factor *b*. The null hypothesis (no

Table 1  
System of higher plant growth forms (after Barkman, 1988; Grime et al., 1988; and Kahmen et al., 2002)<sup>a</sup>

Growth form	Description	Species included
Rhizomatose and hemicespitose grasses	Graminoid herbs with long rhizomes growing in smooth mats or both short and long rhizomes present and plant growing in uneven, lumpy mats	<i>Arrhenatherum elatius</i> , <i>Avenula pubescens</i> , <i>Brachypodium pinnatum</i> , <i>Briza media</i> , <i>Carex caryophyllea</i> , <i>C. flacca</i>
Cespitose grasses	Graminoid herbs with no or short rhizomes only and many stems arranged closed together growing in mostly isolated tussocks	<i>Danthonia decumbens</i> , <i>Festuca lemanii</i> , <i>Koeleria macrantha</i> , <i>Sesleria caerulea</i>
Decumbentes	Forbs with long, prostrate or decumbent stems	<i>Anthyllis vulneraria</i> , <i>Campanula rotundifolia</i> , <i>Galium pumilum</i> , <i>Galium verum</i> , <i>Hippocrepis comosa</i> , <i>Lotus corniculatus</i> , <i>Polygala comosa</i> , <i>Teucrium chamaedrys</i> , <i>Thymus praecox</i> , <i>T. pulegioides</i>
Erectae rosulatae	Erect forbs with basal leaves only	<i>Cirsium acaule</i> , <i>Fragaria viridis</i> , <i>Hieracium pilosella</i> , <i>Leontodon hispidus</i> , <i>Plantago lanceolata</i> , <i>P. media</i> , <i>Platanthera chlorantha</i> , <i>Primula veris</i> , <i>Taraxacum sect. Vulgaria</i> , <i>Viola hirta</i>
Erectae scaposorosulatae	Erect forbs with both stem leaves and a differentiated basal rosette present	<i>Agrimonia eupatoria</i> , <i>Carlina vulgaris</i> , <i>Centaurea scabiosa</i> , <i>C. jacea s. l.</i> , <i>Digitalis lutea</i> , <i>Gentianella germanica</i> , <i>Knautia arvensis</i> , <i>Ophrys insectifera</i> , <i>Orchis mascula</i> , <i>Pimpinella saxifraga</i> , <i>Potentilla neumanniana</i> , <i>Sanguisorba minor</i> , <i>Scabiosa columbaria</i> , <i>Stachys officinalis</i> , <i>Tragopogon pratensis</i>
Erectae scaposae	Erect forbs with only stem leaves present	<i>Achillea millefolium</i> , <i>Bupleurum falcatum</i> , <i>Epipactis atrorubens</i> , <i>Hypericum perforatum</i> , <i>Linum catharticum</i> , <i>Origanum vulgare</i> , <i>Prunella laciniata</i>
Dwarf shrubs	Many-stemmed woody plants less than 1m high	<i>Genista tinctoria</i> , <i>Genistella sagittalis</i> , <i>Helianthemum nummularium</i>
Shrubs	Many-stemmed woody plants 1–5 m high	<i>Crataegus monogyna</i> , <i>Prunus spinosa</i> , <i>Rhamnus cathartica</i> , <i>Rosa canina</i>

<sup>a</sup> Nomenclature follows Lambinon et al. (1993)

differences due to mowing regime), with two degrees of freedom, was tested against the mean square of the nested factor,  $MS_{ba}$ , with three degrees of freedom, by employing the anova procedure implemented by SAS 8e.

In order to test whether bryophyte species composition differed among treatments, if vascular vegetation structure explained a significant amount of variation in bryophyte species composition, and to discover how bryophyte species segregate depending on mowing regime and vegetation structure, linear combinations of these explanatory variables (i.e., mowing regime and canopy structure, including mean herb height and cover and cover of each of the eight growth forms of the vascular flora) were constructed by redundancy analysis (RDA). Considering short ecological gradients underlying subtle changes in community patterns due to a decade of contrasting mowing regimes, this constrained ordination technique indeed seemed appropriate with regard to its efficiency to treat matrices of species with monotonic response curves (ter Braak, 1987). The RDA was performed on standardized species cover  $x_i^0 = (x_i - \bar{x})/\sigma_i$  so that abundant species with high variances did not unduly influence the constrained ordination. As the standardization gave an equal weight to each species, rare species (see above), whose occurrence cannot be significantly related to the set of explanatory variables, were removed from the analysis. Graphic representations of both species and plots along the axes of explanatory variables were obtained using ADE-4 (Thioulouse et al., 1997).

### 3. Results

Average bryophyte species number per quadrat did not significantly differ depending on mowing regime (Table 2). Mean cover of *Scleropodium purum* reached about 80% in mown plots and was significantly higher than in control plots where it reached about 25%. *Plagiommium affine* exhibited the reverse trend and reached a significantly higher cover in control plots than in mown plots. Cover of all other individual species did not significantly vary depending on mowing regime.

In a multivariate context, however, different species patterns were revealed along two main gradients of mowing regime and vegetation structure. The first two axes of the redundancy analysis using mowing regime and vegetation structure to explore bryophyte species patterns explained 41% of the total floristic variance and 55% of the relationship between the floristic data and the explanatory variables. RDA1 opposed the control plots and the mown plots (Figs. 1 and 2). Associated vegetation features included mean herb height and cover in shrubs and rhizomatose to hemicespitate grasses, which were opposed to cover in cespitate grasses. RDA2 opposed the plots mown during and

outside the growth season. Associated vegetation features included cover in *Erectae scaposae* that were opposed to *Erectae rosulatae*.

Along RDA1, *Plagiommium affine*, *Eurhynchium striatum*, and *Ctenidium molluscum* were opposed to *Scleropodium purum* and *Dicranum bonjeanii*. Along RDA2, *Dicranum bonjeanii*, *Hypnum lacunosum*, and *Hylocomium splendens* were opposed to *Lophocolea bidentata* and *Fissidens dubius* (Fig. 3).

### 4. Discussion

Overall species composition at the study site was similar to that documented for other mesophilous calcareous grasslands of western Europe (Watson, 1960; Marstaller, 1979; During and Willems, 1986; Rodwell, 1992; Werner, 1992; Nebel and Philippi, 2000). However, certain species that can be locally common in mesophilous grasslands e.g., *Callergonella cuspidata* (Watson, 1960) and *Entodon concinnus* (Werner, 1992; Nebel and Philippi, 2000), are not of frequent occurrence in the grasslands of southern Belgium and were not observed. Therefore, bryophyte species richness, which reached about seven species per m<sup>2</sup> on average in the mown plots, was within or slightly below the range documented for mown calcareous grasslands (van Tooren et al., 1990).

Quite surprisingly however, species richness per m<sup>2</sup> was not significantly less in the control plots than in the mown plots. This contrasts at first sight with previous observations on the negative influence of shrub encroachment after cessation of management practices on moss species diversity (e.g., van Tooren et al., 1991; During and van Tooren, 2002). In the control plots, a number of grassland species were able to survive within a grassy-shrubby fringe 15 years after shrub cutting.

Table 2

Two-way analysis of variance of species number and species cover per quadrat depending on mowing regime

Dependent variable	m1 <sup>a</sup>	m2 <sup>a</sup>	m3 <sup>a</sup>	P
Species number/quadrat	7.5	7.1	5.8	> 0.05
<i>Campyliadelphus chrysophyllus</i>	<1	<1	0	> 0.05
<i>Ctenidium molluscum</i>	1	3	7	> 0.05
<i>Dicranum bonjeanii</i>	3	13	<1	> 0.05
<i>Eurhynchium striatum</i>	<1	<1	<1	> 0.05
<i>Fissidens dubius</i>	<1	1	<1	> 0.05
<i>Hylocomium splendens</i>	10	14	13	> 0.05
<i>Hypnum lacunosum</i>	2	4	<1	> 0.05
<i>Lophocolea bidentata</i>	<1	<1	<1	> 0.05
<i>Plagiommium affine</i>	<1	0	1	< 0.05
<i>Rhytidiadelphus squarrosus</i>	1	<1	<1	> 0.05
<i>Scleropodium purum</i>	83	78	26	< 0.05

<sup>a</sup> m1, m2, m3 are the mean values of the dependent variable in the plots mown outside the growth season, during the growth season, and in the control plots, respectively.

Experimental results indeed confirm that growth of certain grassland species is hardly affected by a decrease in light quantity and change in light quality associated with a tall and dense herb canopy (van der Hoeven et al., 1998). Apparently, the lower photosynthetic rate at low irradiance is compensated by more favourable water conditions (Bates, 1988). This suggests that there might be a time-lag of at least 20 years before cessation of mowing results in a significant decrease in species number per  $m^2$ .

Although cessation of mowing over a decade did not result in significant differences in species number per quadrat, clear community patterns were revealed in a multivariate context. These patterns correlated to mowing regime and structure of the vascular vegetation, a figure already observed at different spatial scale between patterns in the bryophyte and vascular vegetation and disturbance regime (Mazzoleni et al., 1993; During and Lloret, 1996).

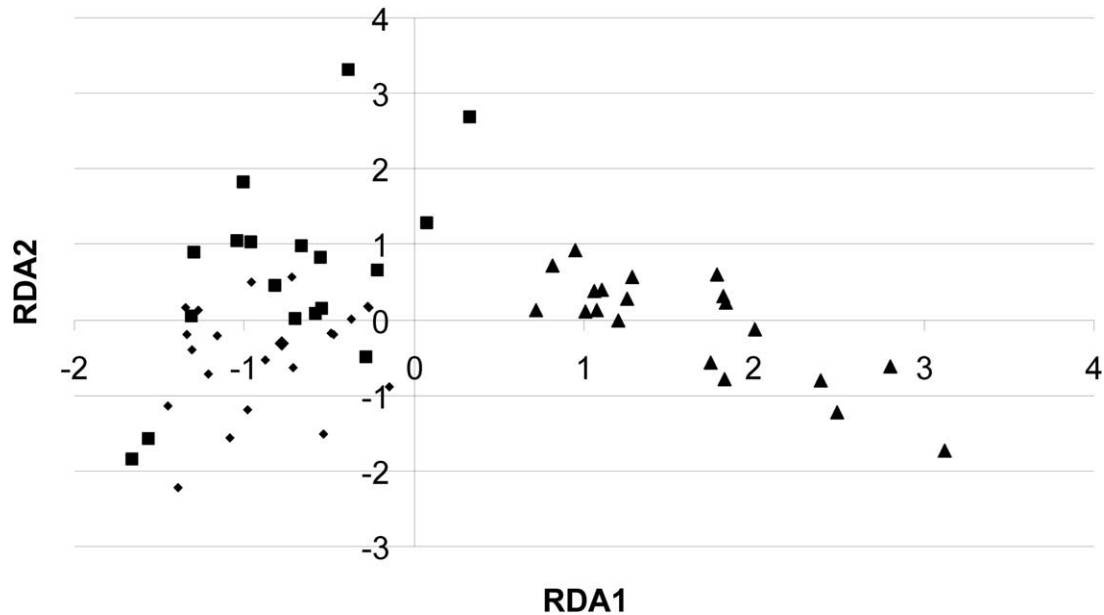


Fig. 1. Score of the 60 individual 1- $m^2$  quadrats along the first two axes of a redundancy analysis between moss species cover, mowing regime, and vascular vegetation structure. ▲: control plots; ■: plots mown outside the growth season of vascular plants; ◆: plots mown during the growth season of vascular plants.

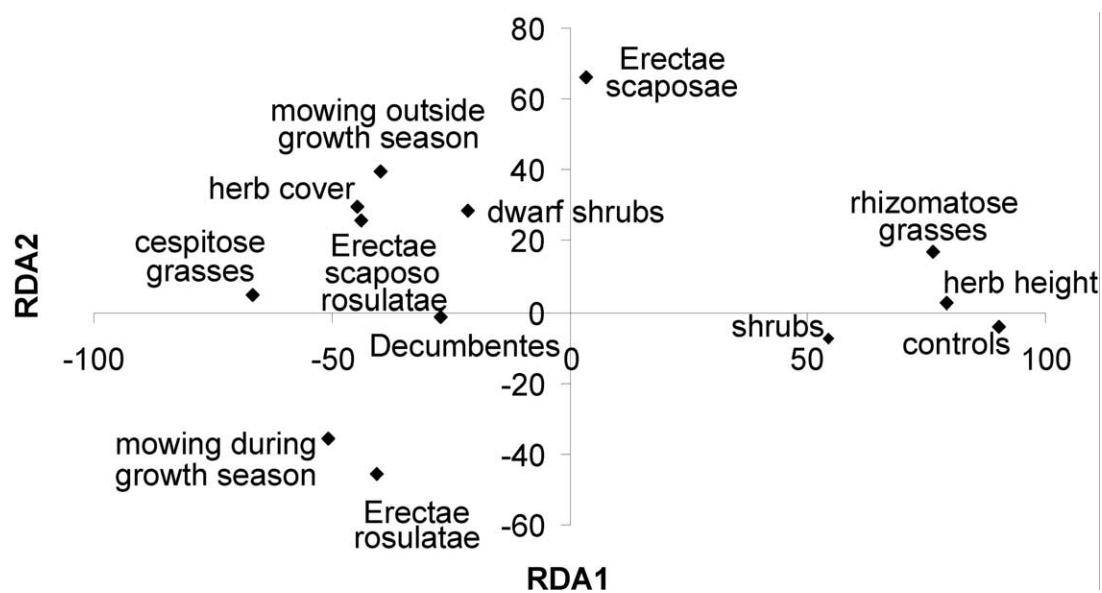


Fig. 2. Score of the explanatory variables along the first two axes of a redundancy analysis between moss species cover, mowing regime, and vascular vegetation structure.



The main community pattern concerned differences among control and mown plots. Control plots were characterized by *Eurhynchium striatum*, a shade-demanding species, and *Plagiomnium affine*, a mesophytic species that had a significantly higher cover in control plots than in mown plots. Mown plots were mostly characterized by a significantly higher cover of the large weft-forming pleurocarp, *Scleropodium purum*, while the occurrence of other large weft- or turf-forming species, such as *Hylocomium splendens*, *Hypnum lacunosum*, and *Dicranum bonjeanii*, tended to be correlated with the mown plots. Conversely, smaller pleurocarps growing appressed to the substrate (*Campyliadelphus chrysophyllus*, *Ctenidium molluscum*), loose turfs of smaller acrocarps (*Fissidens dubius*), dense, small cushions (*Weissia brachycarpa*), and open turfs (*Bryum* spp.), which frequently occur in mesophilous calcareous grasslands of western Europe (Watson, 1960; Marstaller, 1979; During and Willems, 1986; Rodwell, 1992; Werner, 1992; Nebel and Philippi, 2000), were also present but did not respond positively to mowing. In addition, many acrocarps of conservation interest (e.g., *Tortula* spp., *Microbryum* spp.), which are typical of more open calcareous grasslands, were lacking.

Mowing indeed resulted in an almost complete herb and moss cover including a few large turf-forming species that may have prevented the presence of other species. The scarce bare soil patches created by rabbits and other small mammals were indeed very ephemeral and mainly colonised by the commonest pioneer species. The latter were represented by frequently fruiting species, such as *Weissia brachycarpa*, and gemmae or tuber-bearing species such as *Bryum bicolor* and *B. rubens*. The spores, tubers or bulbils produced by these “gap-detecting” species, which are presumably recruited from

the diaspore bank in the soil (During and ter Horst, 1983), allow a fast development as soon as growth conditions become favourable again (During, 1992). Hence, these species randomly occurred at recently disturbed places and were consequently not correlated with the mowing regime.

Similarly, the thick moss turf that thrived in the mown plots may have hampered the development of species characteristic for calcareous grasslands, such as *Ctenidium molluscum* and *Fissidens dubius*, which did not seem to have been favoured by mowing in our experiment. Although the importance of interspecific competition has been debated in bryophytes (see Bates, 1998, for review), it has been documented in a number of situations based on field observations (Li and Vitt, 1995); comparisons of observed patterns with those expected under a neutral model (Wilson et al., 1995); and greenhouse experiments (Zamfir and Goldberg, 2000). *Scleropodium purum* indeed is one of the rare competitors among bryophytes (Grime et al., 1990) and may outcompete smaller species such as *Ctenidium* in mown grasslands where *Scleropodium* often reached an almost 100% cover.

Within the mown plots, difference in mowing season resulted in subtle species patterns, where the hygrophytic leafy hepatic, *Lophocolea bidentata*, was opposed to *Dicranum bonjeanii*, *Hylocomium splendens*, and *Hypnum lacunosum*. Mowing during the growth season resulted in the lowering of the herb canopy. A number of erect forbs indeed had a significantly higher cover in plots mown outside the growth season than in plots mown during the growth season. Mowing during the growth season probably reduced seed production and hence regeneration of a number of erect forbs. This is especially true for strictly biennial species such as *Linum*

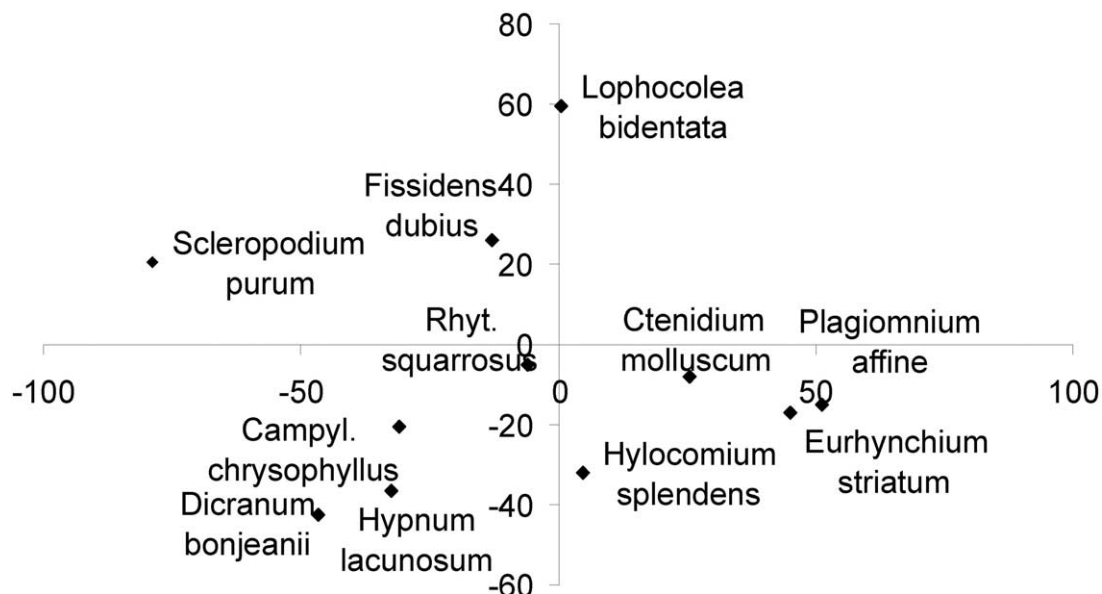


Fig. 3. Species score along the first two axes of a redundancy analysis between moss species cover, mowing regime, and vascular vegetation structure.

*catharticum* whose survival is directly linked to annual recruitment. Other erect forbs, such as *Pimpinella saxifraga*, are perennial but have a short longevity (Grubb, 1990). The lowering of the herb canopy during the driest season of the year may disturb the under-canopy humid microclimate and potentially affecting mesophilous species. Conversely, mowing the herb layer during the spring or the fall, i.e., the period of highest photosynthetic activity for bryophytes (During, 1990), may increase the amount of light reaching the bryophyte layer when drought is a less limiting factor. Such a temporary increase in light may stimulate the growth of mosses such as *Fissidens dubius* (Rincon and Grime, 1989). By contrast, the lower herb canopy in plots mown during the growth season seemed to favour the growth of large mosses, including *Dicranum* and *Hylacomium*. These mosses may benefit from the thinning of the herb layer, especially in places where small forbs with rosettes dominate, while their large weft-forming habit enhances drought tolerance through water retention within the weft (Bates, 1998).

## 5. Conclusion

Cessation of mowing over a decade in a mesophilous calcareous grassland correlated with difference in bryophyte communities but did not result yet in lower species richness in 1 m<sup>2</sup> plots. Indeed, a number of grassland species seem able to tolerate a tall herb canopy. Mowing resulted in almost continuous herb and moss layers that are unfavourable for a number of annual bryophytes, many of which are of great conservation interest. The almost complete moss cover may also have a negative impact on short-lived forbs of conservation interest such as *Gentianella germanica* in terms of predation of seeds after dispersal (van Tooren, 1988), emergence, and establishment of seedlings (Keizer et al., 1985; Zamfir, 2000).

Together with previous assessments of the effects of management practices on bryophytes (Bergamini et al., 2001), but also on vascular plants (e.g., Schlapfer et al., 1998; Oostermeijer et al., 2002), these results suggest that mowing, which seems to be the most effective management strategy to conserve a few taxa such as orchids (Poschlod and WallisDeVries, 2002), may not represent the optimal practice to conserve the global biological richness in calcareous grasslands. Alternatively, grazing, which opens the grass and moss layers, is likely to increase the number of species, especially the number of gap-detecting colonists (van Tooren et al., 1990) that are often of great conservation interest. However, the optimum grazing pressure for bryophytes still needs to be documented in different grassland kinds, as overgrazing in exposed grasslands may result in a dramatic reduction of the herb canopy with sub-

sequent change of mesoclimate and spread of xerophytic species of low conservation interest (Vanderpoorten, 1995).

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