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Effects of nature management practices on the bryophyte flora of grassland and heathland in Drenthe, The Netherlands

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SUMMARY

A study was carried out on the effects of hay-making, hay-making after sod removal, and grazing with different intensities on the bryophyte flora in a moist grassland dominated by *Holcus lanatus* and in a very wet grassland dominated by *Juncus effusus*. The effects of grazing and the abandoning of a heathland area were also compared. The bryophytes were recorded in 1972, 1976 and 1983. In the grazed and the cut plots in the moist grassland area the average number of bryophytes and the degree of cover did not differ, but in the cut plots the degree of cover of bryophytes characteristic for litter became smaller. In the grazed plots, in which the vascular plant composition diverged with the grazing intensity, the bryophyte flora did change, but not diverge. After sod cutting mainly colonist species were present initially, but after 10 years, the number of perennials had increased considerably. In the cut plots in which sods had been removed the degree of cover of bryophytes, especially colonists, became greater than in the cut plots in which sods had not been removed. In the grazed and the cut plots in the very wet grassland area the average number of bryophytes did not diverge, but in the cut plots the degree of cover became highest and the proportion of litter species became smallest. The number of bryophytes remained high in the grazed heathland, but declined in the abandoned area, whereas the degree of cover decreased in both areas. Several species characteristic for heathland disappeared in the grazed area, whereas all 'heathland-species' disappeared in the abandoned area, which turned into woodland.

Key-words: bryophyte flora, grassland, heathland, nature management.

INTRODUCTION

Different management practices have been compared with respect to their effects on the restoration of species-rich grasslands, mainly in The Netherlands (Oomes & Mooi 1981, Willems 1983) and in Germany (Dierschke 1985, Schreiber & Schiefer 1985). These studies are, however, concerned with the vascular plants and give little information about the changes in species composition of the bryophyte flora.

In earlier studies, the effects of grazing on the species composition of vascular plants were recorded in a previously fertilized grassland and also in a fenced-in heathland.

Haymaking and sod removal were carried out in the grassland area for comparison, whereas the grazed heathland was compared to an abandoned area (Bakker *et al.* 1983, Bakker *et al.* 1984, De Leeuw & Bakker 1986). The management practices and local differences with respect to grazing intensity resulted in different vegetational structures, namely heavily grazed short turf (including bare soil) and lightly grazed tall stands (with litter accumulation). In the short turf a great deal of light can reach the soil and colonist moss species can be found on the bare soil (During 1979). In the tall stands with litter accumulation, little light can reach the soil and this hampers the performance of many bryophytes (Mägdefrau 1982, Proctor 1982, Willems 1983, Welch 1984).

This study aims to quantify changes in bryophytic species composition in relation to changes in herbaceous species composition under different management practices.

MATERIALS AND METHODS

In 1972 a sheep-grazing experiment was initiated in a marginal grassland and heathland area, the 'Westerholt' (6°10'NL, 53°01'EL) in the province of Drenthe (The Netherlands). The fenced-in study area included 3 ha of *Calluna vulgaris/Erica tetralix* heathland, 2 ha of deciduous woodland (*Betula* spp. and *Salix* spp.) and 6 ha of pasture land which was originally heathland, but which had been ploughed and sown to grass in the 1950s. The grassland received fertilizer applications until 1971 and was used for hay production. It was subsequently grazed by cattle. No fertilizers have been applied since 1971. In October 1972 sheep were introduced to graze the whole area at an average stocking rate of 3 sheep ha^{-1}. Twenty-five sheep grazed during the period from July to December and 40 between January and July. Since 1980 the area has received a winter rest period from grazing of 2 months.

The experimental lay-out in the terrain allowed for comparison with a non-grazed area in the heathland and a hay-making area in the grassland. In May 1973 the sods were removed in part of the hay-making area. Hay-making was done in July or in August.

Changes in the vegetation were recorded according to the decimal scale (Londo 1975) in 111 permanent plots of 4 m^2 each. These plots were arranged into subsets, some of which are discussed in this study.

In moist grassland (groundwater tables did reach 10–20 cm below soil surface level) dominated by *Holcus lanatus*, hay-making ($n=4$), hay-making after sod removal ($n=2$) and grazing ($n=26$) were compared. The grazed plots were arranged into heavily grazed ($n=4$), lightly grazed ($n=12$) and intermediately grazed ($n=10$). Grazing intensities were estimated by the degree of litter cover (Bakker *et al.* 1984) and the height of the canopy (Ter Heerdt *et al.* 1986).

In wet grassland (inundated for 4 winter months) hay-making ($n=4$) and lightly grazing ($n=8$) were compared.

In the species-rich heathland characterized by *Erica tetralix*, *Dactylorhiza maculata*, *Gentiana pneumonanthe*, *Carex panicea* and *Arnica montana*, lightly grazing ($n=12$) and abandoning ($n=2$) were compared.

The procedure resulted in eight subsets in 1972, nine subsets in 1976 and nine subsets in 1983. An average relevé was composed from the permanent plot data in each subset. The 26 average relevés were clustered (a group average clustering) and the resulting clusters (at 60% dissimilarity) were arranged into a synoptic table.

The bryophytes were recorded in September–October 1972 (unpublished data A.K. Masselink), in April–June 1976 (Hofs 1978) and in the same season in 1983 by the first

author. The date on phanerophytes was initially recorded by the second author or derived from Veldman (1983), De Leeuw & Bakker (1986), Ter Heerdt *et al.* (1986) and Schutter *et al.* (1987).

The nomenclature of phanerophytes is according to Van der Meijden *et al.* (1983) and that of bryophytes to Margadant & During (1982).

The following attributes were quantified for each subset of permanent plots:

(i) the average number of bryophytes in each of the life strategies perennial, shuttle and colonist species according to During (1979),
(ii) the mean degree of cover of all bryophytes together,
(iii) the relative proportion in the subsets of grassland permanent plots of species characteristic for a litter substrate (see Furness & Grime 1982a) and for bare soil or inundated habitats using the habitat descriptions mentioned by Landwehr (1966, 1980), Smith (1978) and Watson (1978); and
(iv) the relative proportion of species characteristic for heathland and non-heathland species (Landwehr 1966, 1980, Smith 1978, Watson 1978).

RESULTS

Grassland

Agrostis capillaris spread a great deal throughout the whole moist grassland, whereas rosette plant species like *Hypochaeris radicata* and *Leontodon autumnalis* only spread in the heavily grazed plots. The average number of bryophytes increased significantly in those plots ($P < 0{\cdot}05$). The degree of cover dropped significantly in all the grazing intensity groups (Fig. 1A–C), which can mainly be attributed to the decrease in *Brachythecium rutabulum* (Table 1). Although more litter was found, the proportion of bryophytes characteristic for litter decreased significantly in the intermediate and lightly grazed plots (Fig. 2A–C).

Hay-making in the moist grassland resulted in a community with *Anthoxanthum odoratum, Leontodon autumnalis* and *Rhinanthus angustifolius* and a significant increase in colonist bryophytes ($P < 0{\cdot}05$) like *Ceratodon purpureus* and *Dicranella heteromalla* (Table 1). Both the degree of cover (Fig. 1D) and the proportion of bryophytes characteristic for litter (Fig. 2D) decreased significantly.

Erica tetralix and *Calluna vulgaris* established after sod removal and many colonist species were initially found (*Ceratodon purpureus, Polytrichum piliferum*), whereas later the number of perennial species increased ($P < 0{\cdot}05$) (Table 1).

The hardly grazed temporarily inundated grassland area became dominated by *Juncus effusus*. A significant decrease in the number of species ($P < 0{\cdot}05$) in particular perennials, namely *Calliergon stramineum* (Table 1) was found. The degree of cover also declined significantly (Fig. 1F). In the cut area, however, *Carex nigra* and *Ranunculus repens* reached high degrees of cover. In this area the degree of cover of bryophytes remained high (Fig. 1G). The proportion of bryophytes characteristic for litter decreased significantly (Fig. 2G).

Heathland

Molinia caerulea spread in the lightly grazed heathland area, whereas the cover of *Erica tetralix* and *Calluna vulgaris* decreased. *Hypnum cupressiforme* var. *ericetorum* maintained itself with a high degree of cover until 1976, but it had disappeared in 1983 (Table 1). The total number of bryophytes remained high, but the average degree of

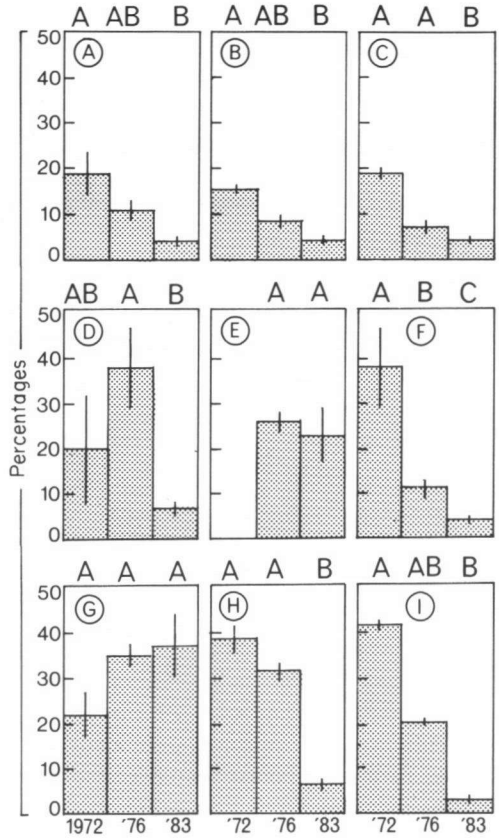

Fig. 1. (A–I) The average percentage of cover (± SE) of bryophytes during the period 1972–1983 under different management practices. Different symbols indicate significant differences ($P < 0{\cdot}05$ according to Student's *t*-test). Confer Table 1 for the management practices.

cover decreased significantly (Fig. 1H). Although the proportion of bryophytes characteristic for heathland did not change, some species did disappear, namely *Sphagnum rubellum* and *Mylia anomala,* whereas others could maintain themselves, namely *Pleurozium schreberi* and *Odontoschisma sphagni.* The abandoned heathland area grew into a *Betula pubescens* woodland, which resulted in a significant decline in the average degree of cover of the bryophytes (Fig. 1I) and the disappearance of several species amongst which were bryophytes characteristic for heathland (Fig. 2I and Table 1).

DISCUSSION

Grazing in grassland

The differences between the management regimes which were imposed on the bryophyte flora in different years are summarized in Table 2. It appeared that prior to the start of the experiment some differences were found between the subsets of permanent plots in the grassland area. Moreover, the bryophyte species composition within subsets sometimes diverged a great deal. This makes it difficult to discuss changes in the level of individual species. Some general trends with respect to the degree of cover, life strategies and 'litter' and 'heathland' species can nevertheless be discerned.

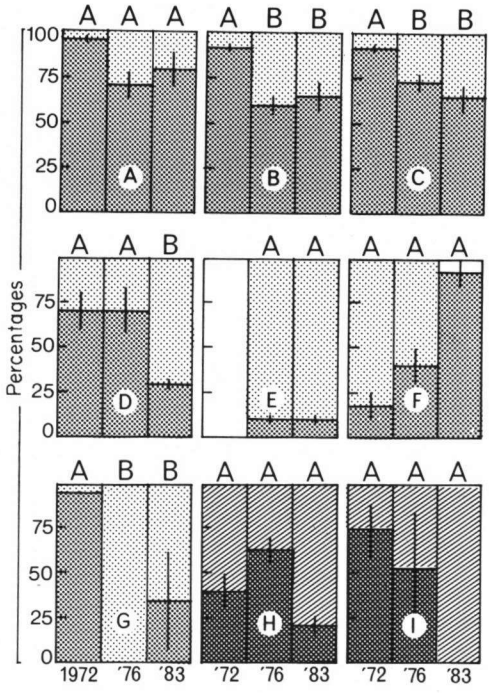

Fig. 2. (A–I) The proportion of percentages of cover (±SE) of bryophyte species characteristic for litter (intermediately dotted), species characteristic for bare soil or inundated habitats (lightly dotted), species characteristic for heathland (heavily dotted) and non-heathland species (hatched). Different symbols indicate significant differences ($P < 0{\cdot}05$ according to Student's *t*-test). Confer Table 1 for the management practices.

In the grazed moist grassland area the vegetation structure varies with the grazing intensity. In the heavily grazed area the vegetation structure is more open and shows more height differences than in the lightly grazed area. The amount of light reaching the soil in the lightly grazed area is only 20% of that in the heavily grazed area (Hendriks 1984). As a consequence of the more varied vegetation structure, more different microhabitats for bryophytes are present in the heavily grazed plots. A greater number of bryophyte species and a higher degree of cover is, therefore, expected in the heavily grazed plots compared to the lightly grazed plots (cf. Watson 1960, Proctor 1982, During & Ter Horst 1983, Willems 1983, Welch 1984, During & Willems 1986). Despite the different vegetation structures no differences could, however, be recorded with respect to the bryophyte flora. An explanation for this discrepancy could be the fact that localities with different grazing intensities often alternate in such a fine-scaled pattern (Bakker *et al.* 1984) in the moist grassland that even in lightly grazed plots often small intensively grazed patches with a short turf are found. It seems, therefore, reasonable to assume that the structure of the lightly grazed area (*c.* 400 gdw litter m^{-2} vs. 100 gdw litter m^{-2} in the heavily grazed area) (Bakker *et al.* 1984) does not (yet) resemble that of an abandoned grassland.

Schiefer (1981) compared the effects of grazing and abandoning during 4 years in 11 plant communities in Germany. He found an increase in the coverage and thickness of litter in eight and no difference in three abandoned sites. The bryophyte coverage was higher in the grazed than in the abandoned area in four sites, the reverse was true in two sites and no difference was found in five sites. The percentage of cover was, however,

Table 1. Synoptic table of the coena (numbers 1–12) occurring in the Westerholt area during the period 1972–1983. The coena found in 1972, 1976 and 1983 are referred to by the letters A–I

Coenon			1	2	3	4	5	6	7	8	9	10	11	12
1972 data*				G	F		A,B,C,D						H	I
1976 data			G		F		A,B,C,D			E			H	I
1983 data				F		G		A,B,C,D	E		I	H		
Number of relevés			4	8	16	3	60	30	2	2	2	12	23	4
	P‡	*Drepanocladus aduncus*	100/3				2/r							
L†	P	*Calliergon cordifolium*		75/1	63/+	33/+	3/r	7/r				8/r	6/r	
	P	*Calliergonella cuspidata*	25/r		63/a	33/a	30/r	10/r	100/+					
L	P	*Brachythecium rutabulum*		38/r	69/+	67/a	100/1	97/+	100/+	100/+		42/r	34/r	25/r
	P	*Drepanocladus fluitans*		25/r	25/+								9/r	
	P	*Leptodictyum riparium*			19/+	33/1	5/r							
	P	*Calliergon stramineum*			19/a		2/r					8/r	9/r	
	P	*Rhytidiadelphus squarrosus*			19/+		5/r	13/r	50/r			8/r		
	P	*Thuidium tamariscinum*			19/r									
	P	*Calliergon* cf. *giganteum*			13/r									
	C	*Leptobryum pyriforme*			13/r		30/r							
L	P	*Eurhynchium praelongum*		13/r			75/+	77/r	100/+	100/+		25/r	14/r	
	S	*Pohlia nutans*			19/r		18/r	43/r	50/r		50/r	42/r	57/r	50/r
	P	*Climacium dendroides*					5/r	10/r						
	P	*Amblystegium serpens*					5/r							
	C	*Riccardia chamedryfolia*					3/r							
	S	*Physocmytrium pyriforme*					3/r							
	C	*Dicranella heteromalla*						27/r	100/+			17/r		
	P	*Mnium hornum*			6/r			17/r					3/r	
L	P	*Lophocolea bidentata*			25/r			7/r				42/r	20/r	
H	C	*Campylopus introflexus*						3/r						
	P	*Polytrichum commune*			13/r		2/r		100/a	100/r		8/r	9/r	
	P	*Atrichum undulatum*			19/r			13/r	100/+	100/+			6/r	
	C	*Ceratodon purpureus*		13/r			27/r	27/r	100/+	100/1			3/r	
	C	*Cephaloziella divaricata*						3/r	100/+					
	C	*Bryum* sp.			6/r		17/r	3/r	50/r	100/+				
	S	*Cephalozia bicuspidata*							50/r				11/r	
	C	*Polytrichum piliferum*							50/+					

C	*Funaria hygrometrica*					100/+					
	Cephaloziella sp.					100/+			3/r		
	Dicranella sp.		3/r			50/r			3/r		
C	*Bryum pallens*		8/r			50/r					
P	*Dicranum scoparium*						100/+	58/r	63/+	25/r	
P	*Hypnum cupressiforme*				50/r		100/+	75/r	46/+		
H P	*Pleurozium schreberi*	6/r	3/r					58/r	46/+	100/+	
P	*Aulacomnium palustre*	13/r	2/r					50/r	54/+	75/r	
H P	*Leucobryum glaucum*							25/r	43/+		
P	*Pseudoscleropodium purum*	19/+						17/r	14/r	50/+	
L P	*Lophocolea heterophylla*	6/r		2/r			50/r	33/r	23/r		
H P	*Odontoschisma sphagni*							25/r	31/r		
P	*Plagiothecium denticulatum*	13/r						17/r	11/r		
P	*Sphagnum palustre*								26/r		
H P	*Calypogeia fissa*	6/r						8/r	20/r		
H P	*Sphagnum tenellum*							8/r	23/r		
H P	*Sphagnum compactum*							8/r	23/r		
H P	*Sphagnum papillosum*	6/r						8/r	17/r		
H P	*Sphagnum rubellum*								17/r		
H P	*Gymnocolea inflata*								14/r		
C	*Campylopus flexuosus*								11/r		
H P	*Mylia anomala*								9/r		
H C	*Campylopus fragilis*								9/r		
H P	*Sphagnum recurvum*							8/r	3/r		
H P	*Hypnum imponens*								6/r		
H P	*Dicranum spurium*								6/r		
H P	*Cephalozia connivens*			3/r					3/r		
P	*Dicranum bonjeanii*							8/r	14/r	50/+	
H P	*Hypnum cupressiforme* var. *ericetorum*								34/a	100/1	

*A: moist grassland, heavily grazed; B: moist grassland, intermediately grazed; C: moist grassland, lightly grazed; D: moist grassland, hay-making; E: moist grassland, hay-making after sod removal (1973); F: very wet grassland, lightly grazed; G: very wet grassland, hay-making; H: species-rich heathland, grazed; I: species-rich heathland, abandoned.

†Litter (L) and heathland (H) species are indicated.

Also the life-strategies according to During (1979) are given. ‡P: perennial; S: shuttle-species; C: colonist.

The occurrence of the species is given in percentages of frequency and in mean percentages (r: < 1; +: 1–5; a: 6–10; 1: 11–20; 2: 21–30 etc.).

Addenda: Species occurring in one relevé—*Mnium affine, Mnium undulatum, Pohlia camptotrachela, Isopaches bicrenatus, Pellia* sp., *Scapania curta, Brachythecium albicans, Mnium affine* var. *rugicum, Plagiothecium* sp., *Lophozia ventricosa.*

Table 2. Comparison of different pairs of management regimes with respect to several criteria concerning the bryophyte flora in 1972, 1976 and 1983

Management regimes	1972							1976							1983						
	Total number of species	Perennial species	Shuttle species	Colonists	Total cover (%)	Cover 'litter' species (%)	Cover 'heathland' species (%)	Total number of species	Perennial species	Shuttle species	Colonists	Total cover (%)	Cover 'litter' species (%)	Cover 'heathland' species (%)	Total number of species	Perennial species	Shuttle species	Colonists	Total cover (%)	Cover 'litter' species (%)	Cover 'heathland' species (%)
Moist grassland																					
intensively grazed vs. hay-making	0	0	0	0	0	>	·	0	0	0	0	<	0	·	0	0	0	0	0	⩾	·
intermediately grazed vs. hay-making	0	0	0	0	0	⩾	·	0	0	0	0	<	0	·	0	0	0	0	0	>	·
lightly grazed vs. hay-making	0	0	0	0	0	⩾	·	0	0	0	0	<	0	·	0	0	0	0	0	⩾	·
hay-making vs. sod removal	·	·	·	·	·	·	·	0	0	0	<	0	>	·	0	⩾	0	0	>	⩾	·
Wet grassland																					
lightly grazed vs. hay-making	>	>	0	0	0	⩽	·	0	0	0	0	<	>	·	0	0	0	0	⩽	0	·
Species-rich heathland																					
intermediately grazed vs. abandoning	0	0	0	0	0	·	0	0	0	0	0	0	·	0	0	0	0	0	0	·	>

>: first regime larger than second regime ($P<0{\cdot}05$), ⩾: idem ($P<0{\cdot}01$ according to Student's *t*-test); 0: not significant; ·: does not apply.

estimated in June or in July which is not the optimal period for mosses (see Al-Mufti *et al.* 1977, Furness & Grime 1982b, Pegtel 1987). It should be kept in mind that the degree of cover of bryophytes can also vary according to the degree of humidity. Little value should, therefore, be attached to small changes in percentages of cover. The number of bryophyte species was highest in the grazed area in four sites, the reverse was true in five sites, whereas no difference was found in two sites (Schiefer 1981). Differences in the number of species were, however, very small like in the present study.

In the lightly grazed very wet grassland area the number of bryophyte species in a plot and the degree of cover of bryophytes have decreased very strongly. In this very wet and sometimes inundated area *Juncus effusus*, which was ungrazed, became dominant and litter accumulated (up to 2000 gdw.m^{-2}). It is expected that only a few species, like the 'litter' species *Brachythecium rutabulum* and *Calliergon cordifolium*, can maintain themselves on such substrata. Van Tooren *et al.* (1987) described a similar situation for abandoned chalk grassland, in which bryophytes are almost absent. They ascribed this to the very high degree of cover of tall grasses in combination with the accumulation of huge amounts of litter.

With respect to the 'litter' species, it should be noted that the descriptions in the literature are not always in agreement. This is especially the case for species that grow on banks of ponds or are submerged. Not too much value should, therefore, be attached to severe changes in the proportion of 'litter' species on the ground of one single species (which is the case in the very wet grassland subsets).

Hay-making and sod removal

In the moist grassland hay-making did result in an increase in the number of species, in particular colonists, but the degree of cover decreased, mainly due to the decline in the 'litter' species *Brachythecium rutabulum*. The increase in the number of colonists and shuttle species conforms to the expectation that the removal of litter during hay-making results in gaps with possibilities for the establishment of colonists and shuttle species (Miles 1973, Hofs 1978, During 1979). The very high degree of cover of bryophytes in the very wet grassland under hay-making may be due to the fact that the mosses are not hampered by vascular plants which start growing late in such a wet and cold environment. The growth of many mosses is, however, optimal at the relatively low temperature conditions of the winter and spring period (Al-Mufti *et al.* 1977, Richardson 1981, Furness & Grime 1982b).

The removal of sods has lead to an invasion of colonists followed by the emergence of perennial species. This is in agreement with records from Miles (1973), Southorn (1977), Gimingham (1978), Hobbs *et al.* (1984), and Forgeard & Tallur (1986) for recolonization of soil after sod removal and burning.

Heathland

The decline in the number and degree of cover of bryophyte species, amongst which species characteristic for heathland, was most marked in the abandoned heathland, which became overgrown with *Betula pubescens* and to a lesser degree in the grazed heathland, which became overgrown with grasses. Gimingham (1978) and Welch (1984) have found similar results in heathland which was becoming overgrown by grasses and they attributed this phenomenon to reduced light supply to the soil and the greater competitive ability of some of the species present amongst others *Brachythecium rutabulum, Eurhynchium praelongum* and *Pleurozium schreberi.*

Comparison of management regimes

In this study species-richness was highest in areas in which the sods were removed. This is, however, a transitional phase. Hay-making and grazing create habitats in which gaps can also be present for colonists and shuttle species provided a frequent hay-making regime and, at least locally, a high grazing intensity exists. During & Willems (1986) prefer grazing to hay-making and abandoning for chalk grasslands because of the higher species-richness in grazed areas. The differences between grazing and hay-making are, however, small (Willems 1983).

In the moist grassland area the degree of cover of bryophytes did not diverge under a grazing and a hay-making regime in this study, whereas in the very wet grassland area hay-making resulted in a much higher cover than a grazing regime (Fig. 1 and Table 2). Also in chalk grassland under hay-making the degree of cover of bryophytes was higher than under a grazing regime; the differences were, however, small (Van Tooren *et al.* 1987, Willems 1983). Probably, hay-making offers better chances for bryophytes, due to the higher light intensity in the winter (growing) season.

The present study shows that in a grassland area both grazing and hay-making can lead to a vegetation with a varied bryophyte composition and that local differences in grazing intensity do not (yet) lead to diverging bryophyte floras after 11 years. In the heathland area only in the grazed plots bryophyte species characteristic for heathland can maintain themselves. From earlier studies (Ter Heerdt *et al.* 1986, Schutter *et al.* 1987) it appears that the same applies to the vascular plants.

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