

Bryophyte vegetation in a wooded meadow: relationships with phanerogam diversity and responses to fertilisation

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Abstract

In the Laelatu wooded meadow in Estonia, famous for its phanerogam diversity, the bryophyte community has been investigated in order to compare its flora and diversity relationships with those of the vascular plant community. Ninety-six bryophyte species were found, 13 of them are hepatics; the majority of the bryophytes are epigeic species common to meadows and forests, including many calciphilous species. Vascular plants and bryophytes display opposite responses to fertilisation. For vascular plants, fertilisation increases the coverage and diminishes the number of species, while for bryophytes it diminishes coverage and increases the number of species. The relationship between the number of species in small plots and the total number of species in the area is similar for vascular plants and bryophytes. No significant changes in the bryophyte community in Laelatu wooded meadow has been detected during the last 30 years.

Nomenclature:

For bryophytes Ingerpuu et al. (1994), for vascular plants Laasimer et al. (1993–97).

Introduction

Areas of exceptional high species richness are interesting from both the theoretical and conservational point of view. Considering the scale-dependence of species richness records (Stoms 1994), it is important to distinguish between species-rich sites of different scale. On a small scale (10 m² and less) some particular types of grassland represent the most species-rich vascular plant communities in the world (Sanders 1995). In a very small number of sites, the number of vascular plant species exceeds 60 species per 1 × 1 m plot – among these, published data exist for Strelets meadow steppe in Russia (Afanaseva & Golubev 1962), and for West-Estonian wooded meadows (Kull & Zobel 1991).

We define a wooded meadow as a natural sparse woodland with a regularly mown herb layer. Wooded meadows were typical and traditional in many areas around the Baltic Sea, but have almost all disappeared due to changes in management regimes during the last

half century (Hægström 1983). The remaining few on calcareous soils have been found to have some of the highest known vascular plant species-richness values on the small scale (Kull & Zobel 1991). It is, however, unclear whether the other components of the ecosystem are also rich in species and whether they contain rare species (e.g., Talvi 1995).

Bryophytes constitute a permanent part of the flora of calcareous grasslands. Variations in the species composition of the bryophyte layer are mainly determined by the same factors that influence the vascular plant community – management regime, topography, bedrock (During 1990), but their relationship to the variation in the vascular plant community has still not been explained completely. Herben (1987) has compared fluctuations in bryophyte and phanerogam communities. There are several studies on the influence of the bryophyte layer on the emergence of seedlings (e.g., Tooren 1990; Hein 1966), and on the effect of the density of the vascular plant community or community gaps

on bryophytes (Jonsson & Esseen 1990). The influence of differences in the management of vegetation on bryophytes has also been described (Brown 1992; Tooren et al. 1988; During & Tooren 1988). During & Tooren (1990) emphasized the possible importance of the mutualistic relationships between bryophytes and other plants. The relationships between species richnesses are less well studied.

Since the 1950s, vascular plant coverage, productivity, phenology, and seed-bank composition have been studied at Laelatu wooded meadow (Hein 1966; Krall & Pork 1970; Kull & Zobel 1991). However, until now data about bryophytes were rather scarce. In 1962–63 the moss vegetation in some plots on Laelatu meadow was described in connection with an experiment on meadow fertilisation, and changes in the bryophyte community were recorded (Kalda & Kannukene 1966). The aims of the present study are (1) to characterise the bryophyte vegetation in the wooded meadow community richest in vascular plant species at Laelatu, (2) to compare diversity trends in bryophyte and vascular plant communities on fertilised and unfertilised ground, and (3) to see if the bryophyte vegetation of some sample plots has changed since 1963.

Study area

Laelatu wooded meadow is situated in the western part of Estonia, close to the Baltic Sea, between the Mõisa, Kase, and Hein bays, and covers an area of about 100 ha. The meadow had regularly mown for over 300 years, but the mown area has now decreased to only ca 15 ha.

The mean temperature for July is 17.0 °C, and for January –5.0 °C. The mean annual precipitation is 500 mm. The soil is a rendzic leptosol with a pH of 6.7–7.2 (Niinemets & Kull 1997), formed on calcareous silurian bedrock. It is characterized by a thin humus layer (15–20 cm) and is relatively poor in available nutrients (Sepp & Rooma, 1970). Soil moisture content varies, both dry and wet meadow sites are represented.

The tree layer (crown projections) covers 30–50% of the ground in typical sites (more open sites or those which have a more closed canopy also exist) and consists of *Quercus robur*, *Betula pendula*, *Betula pubescens*, *Fraxinus excelsior* a.o. The undergrowth includes *Fraxinus excelsior* and *Populus tremula*, with many species of shrubs (*Corylus avellana*, *Sorbus aucuparia*, *Rhamnus cathartica*, *Viburnum opulus*,

a.o.). The field layer is very rich in species, being one of the richest known (at least in temperate Eurasia) at a small scale – the number of vascular plant species on 1 × 1 m plot exceeds 60 (Kull & Zobel 1991), with a recorded maximum of 68 species. There are almost no dominant species. Characteristic species are *Sesleria coerulea*, *Filipendula hexapetala*, *Festuca rubra*, *F. ovina*, *Carex flacca*, *Succisa pratensis*, *Prunella vulgaris*, *Plantago lanceolata*, *Convallaria majalis*, *Centaurea jacea*, *Cirsium acaule* (Krall & Pork 1970). The vascular plant flora in Laelatu wooded meadow (without adjacent habitats) contains 371 species.

Methods

In 1961, a meadow fertilisation experiment was set up by K. Pork at a typical, quite uniform and relatively dry site in Laelatu wooded meadow. The main experiment used twelve 10 × 30 m permanent plots that are still used for long-term succession research. Nine plots were fertilised during the period 1961–1981. Since 1982, no plots were fertilised. The plots were mown every year in July, and the hay was removed. In the present study, we analysed four of these plots – two fertilised plots F₁ and F₂ (numbers 4 and 11 of the original experiment, which have received 3.5 g m⁻² nitrogen, 2.6 g m⁻² phosphorus and 5 g m⁻² potassium annually), and two controls – C₁ and C₂ (6 and 10, respectively). The plots represent very old wooded meadow vegetation, which has been regularly mown without any great changes during at least the last three centuries. The only difference between the F plots and controls has been the 20 year period of fertilisation. F₁ and C₁ are close together and are 200 m from the other close pair F₂ and C₂. At the end of June 1995, three sample plots (a to c) of 1 × 1 m in each of the larger plots were used for the description of the bryophyte vegetation. The above-ground biomass and the number of vascular plant species were measured from 20 randomly placed 20 × 7.5 cm sample plots within the 10 × 30 m plot. The Student's *t*-test was used for statistical analysis.

Table 1. Bryophytes of Laelatu wooded meadow. The frequency is marked as following: C – common; O – occasional; R – rare; not-marked – recorded only in literature or herbarium data. The pH classes represent the ecological indices by Düll (1991) (1 – pH<4; 3 – pH 4–5; 5 – pH 5–6; 7 – pH 6–6.9; 9 – pH>6.9; 2, 4, 6, and 8 represent intermediate values), and substrata reaction groups by Apinis & Diogucs (1933) and Apinis & Lācis (1936) (I hyperacidophilous, II mesoacidophilous, III acidophilous, IV neutroacidophilous, V neutromesoacidophilous, VI euryionic, VII hypoacidophilous, VIII neutrohypoacidophilous, IX neutrophilous, X meioeuryionic, XI basihypoacidophilous, XII basineutrophilous, XIII basiphilous).

	pH		Frequency
	Alpinis	Düll	
EPIGEIC			
<i>Atrichum undulatum</i>	III	4	
<i>Aulacomnium palustre</i>	VI	3	O
<i>Barbula convoluta</i>	XI	6	R
<i>Barbula unguiculata</i>	XII	7	R
<i>Brachythecium oedipodium</i>	III	3	C
<i>Brachythecium rivulare</i>	XI	5	R
<i>Brachythecium salebrosum</i>	V	5	O
<i>Bryum argenteum</i>	XI	6	R
<i>Bryum caespiticium</i>	V	6	O
<i>Bryum inclinatum</i>	VII	7	R
<i>Bryum pallescens</i>	–	7	R
<i>Bryum pseudotriquetrum</i>	X	7	R
<i>Calliergonella cuspidata</i>	X	7	
<i>Campylium stellatum</i>	XI	7	C
<i>Ceratodon purpureus</i>	VI	–	C
<i>Chiloscyphus pallescens</i>	II	7	O
<i>Cirriphyllum piliferum</i>	X	6	C
<i>Climacium dendroides</i>	X	5	C
<i>Conocephalum conicum</i>	VI, X	7	R
<i>Ctenidium molluscum</i>	XII	8	C
<i>Dicranum polysetum</i>	III	5	C
<i>Dicranum scoparium</i>	III	4	C
<i>Didymodon rigidulus</i>	XII	7	R
<i>Ditrichum flexicaule</i>	XI	9	O
<i>Drepanocladus aduncus</i>	VI	7	O
<i>Drepanocladus cossonii</i>	X	8	C

Table 1. Continued

	pH		Frequency
	Alpinis	Düll	
<i>Drepanocladus lycopodioides</i>	XII	9	
<i>Encalypta vulgaris</i>	XI	8	R
<i>Eurhynchium angustirete</i>	–	7	O
<i>Eurhynchium hians</i>	VIII?	7	O
<i>Eurhynchium praelongum</i>	XI	5	
<i>Fissidens adianthoides</i>	VI, X	5	C
<i>Fissidens taxifolius</i>	XI	7	O
<i>Funaria hygrometrica</i>	X	6	O
<i>Homalothecium lutescens</i>	XI	8	C
<i>Hylocomium splendens</i>	IV	5	C
<i>Lophocolea minor</i>	V	8	
<i>Marchantia polymorpha</i>	VI	5	R
<i>Mnium stellare</i>	X	7	R
<i>Plagiochila asplenioides</i>	IV	6	O
<i>Plagiochila porelloides</i>	–	7	O
<i>Plagiomnium affine</i>	X	5	C
<i>Plagiomnium elatum</i>	–	6	R
<i>Plagiomnium ellipticum</i>	–	3	O
<i>Plagiomnium undulatum</i>	V	6	C
<i>Pleurozium schreberi</i>	IV	2	C
<i>Polytrichum piliferum</i>	III	2	
<i>Ptilidium ciliare</i>	II	2	
<i>Racomitrium canescens</i>	III	6	R
<i>Rhizomnium punctatum</i>	V	4	O
<i>Rhodobryum roseum</i>	II	7	O
<i>Rhytidiadelphus squarrosus</i>	III	5	O
<i>Rhytidiadelphus triquetrus</i>	IV	5	C
<i>Scleropodium purum</i>	III	5	C
<i>Scorpidium scorpioides</i>	XI	9	
<i>Thuidium abietinum</i>	XI	7	O
<i>Thuidium delicatulum</i>	II?	7	C
<i>Thuidium philibertii</i>	X	7	C
<i>Thuidium recognitum</i>	X	6	O
<i>Thuidium tamariscinum</i>	IV	4	
<i>Tomentypnum nitens</i>	X	8	R
<i>Tortula ruralis</i>	X	6	C
<i>Warnstorfia fluitans</i>	III?	1	R
EPILITHIC			
<i>Barbilophozia barbata</i>	III	5	O
<i>Brachythecium populeum</i>	XI	7	O
<i>Dicranum fuscescens</i>	III	2	
<i>Grimmia pulvinata</i>	VIII	7	R

Table 1. Continued

	pH		Frequency
	Alpinis	Düll	
<i>Hedwigia ciliata</i>	II	2	C
<i>Metzgeria furcata</i>	–	6	O
<i>Orthotrichum anomalum</i>	XII	8	R
<i>Orthotrichum rupestre</i>	XI	6	R
<i>Orthotrichum speciosum</i>	II	5	O
<i>Paraleucobryum longifolium</i>	II	1	O
<i>Schistidium apocarpum</i>	X	7	C
EPIPHYTIC			
<i>Amblystegium serpens</i>	XI	6	C
<i>Amblystegium subtile</i>	IX	6	R
<i>Anomodon longifolius</i>	XI	8	R
<i>Antitrichia curtipendula</i>	II,(IV)	6	O
<i>Brachythecium velutinum</i>	V	6	R
<i>Campylium polygamum</i>	XII	4	O
<i>Dicranum montanum</i>	I	2	C
<i>Frullania dilatata</i>	II	5	R
<i>Homalia trichomanoides</i>	VII	7	O
<i>Homalothecium sericeum</i>	XII	7	R
<i>Hypnum pallescens</i>	II?	2	O
<i>Leucodon sciuroides</i>	X	6	C
<i>Plagiothecium laetum</i>	III	2	O
<i>Pseudoleskella nervosa</i>	XII	6	O
<i>Pylaisia polyantha</i>	VIII	7	O
<i>Radula complanata</i>	II	7	R
<i>Sanionia uncinata</i>	V	3	C
EPIXYLIC			
<i>Aulacomnium androgynum</i>	III, IV	2	R
<i>Hypnum cupressiforme</i>	IV	4	C
<i>Lophocolea heterophylla</i>	III	3	O
<i>Pohlia nutans</i>	III	2	R
<i>Ptilidium pulcherrimum</i>	–	2	C

The present list of bryophytes in Laelatu wooded meadow has been compiled from literature (Kalda & Kannukene 1966; Nurk 1983) and the herbarium of the Institute of Zoology and Botany, in addition to the collections of the authors from 1987 and 1995 from the whole area and from the 12 experimental plots described above. Three frequency classes have been used based on the estimations of collectors. The

unpublished material of L. Kannukene from 1975 and M. Leis from 1989 has also been used.

Results

The total number of bryophyte species found at Laelatu is 96 (thirteen of which are hepatics); they belong to 30 families and 61 genera (Table 1). The majority of the species (63) are epigeic. According to the existing ecological classifications (Apinis & Diogucs 1933; Apinis & Lācis 1936; Düll 1991), nine calciphilous (seven of them epigeic) and 26 acidophilous (14 of them epigeic) species were found, the other species having a wide amplitude, being either neutral, or lacking precise data. About one third of the species prefer moist habitats (meso-hygro-, hygro- and hydrophytes), and one third prefer dry habitats (xero- and xero-mesophytes), the others are mesophytes or have a wide amplitude (Ingerpuu et al. 1994). Among the epigeic species, the ratio between moisture-preferring species and dry-habitat species is approximately 2:1.

The number of bryophyte species found within the experimental plots (which represent an area of 0.12 ha) in this study was 21, whereas the number of vascular plant species found from the same area was 94.

The number of bryophyte species in previously fertilized (F) plots was considerably higher than in control (C) plots, which is especially noticeable when using the pooled data (Table 2, Table 4).

The difference in bryophyte species richness in the F and C plots is due to the presence of additional species in the F plots. C plots contained only one species which was not present in the F plots whereas 12 species found in the F plots were absent from the C plots (Table 3).

The F plots had more species than the C plots, whereas the opposite was the case for vascular plants (Table 4). The F plots have lower bryophyte cover than the C plots (only in one case did the cover value exceed 55 in the F plots, and only once was it lower than 60 in the C plots), whereas the aboveground biomass and cover of vascular plants is higher in the F than in the C plots.

Discussion

The bryoflora of Laelatu wooded meadow includes many ecologically quite different species. The occurrence of so many species with different ecological requirements can be explained by the existence of

Table 2. Species list and the cover values (%) of sample plots. F – fertilised, C – control plots.

	F _{1a}	F _{1b}	F _{1c}	F _{2a}	F _{2b}	F _{2c}	C _{1a}	C _{1b}	C _{1c}	C _{2a}	C _{2b}	C _{2c}
<i>Amblystegium serpens</i>	1											
<i>Barbula convoluta</i>	+	+										
<i>Barbula unguiculata</i>	+											
<i>Brachythecium salebrosum</i>		1		+								
<i>Bryum</i> sp.	+											
<i>Campylium stellatum</i>						+						
<i>Chiloscyphus pallescens</i>						+						
<i>Cirriphyllum piliferum</i>			+									
<i>Eurhynchium hians</i>		+			+						+	
<i>Fissidens taxifolius</i>	+					+						+
<i>Hylocomium splendens</i>			10		10		15	25	45	5	10	
<i>Plagiochila asplenioides</i>					+	+		+	+	+	+	
<i>Plagiomnium affine</i>	5		1	1	1							
<i>Plagiomnium undulatum</i>	15	5	5		+	5						
<i>Pleurozium schreberi</i>									5			
<i>Rhodobryum roseum</i>					+							
<i>Rhytidiadelphus squarrosus</i>	5	40	35	+	20		15	5	5			
<i>Rhytidiadelphus triquetrus</i>		5	5	40	10	45	30	15	5	60	55	55
<i>Sanionia uncinata</i>						+						
<i>Scleropodium purum</i>	+	+	5	10	10	10	5	5	+	1	5	5
<i>Thuidium delicatulum</i>				5	+	1						1
Total bryophyte cover	25	50	55	55	50	60	60	50	60	65	70	60
Number of species	9	7	7	6	10	9	4	5	6	4	6	3

Table 3. Comparison of species presence and absence in F (fertilised) and C (control) plots.

	Absent in C		Absent in F	
	Present in F ₁ and F ₂	Present in F ₁ or F ₂	Present in C ₁ or C ₂	Present in C ₁ and C ₂
<i>Brachythecium salebrosum</i>	+			
<i>Plagiomnium affine</i>	+			
<i>Plagiomnium undulatum</i>	+			
<i>Amblystegium serpens</i>		+		
<i>Barbula convoluta</i>		+		
<i>Barbula unguiculata</i>		+		
<i>Bryum</i> sp.		+		
<i>Campylium stellatum</i>		+		
<i>Chiloscyphus pallescens</i>		+		
<i>Cirriphyllum piliferum</i>		+		
<i>Rhodobryum roseum</i>		+		
<i>Sanionia uncinata</i>		+		
<i>Pleurozium schreberi</i>			+	

various microniches with different moisture and pH conditions at the site. The majority of the species are common epigeic meadow and forest species (Table 1). A large number of species characteristic to moist and

paludifying meadows can be found here (*Drepanocladus* spp., *Calliargonella cuspidata*, *Aulacomnium palustre*, *Fissidens adianthoides*, *Tomentypnum nitens*, *Plagiomnium affine*). The occurrence of calciphilous

Table 4. Vascular plant and bryophyte community parameters in F (fertilised) and C (control) plots. *t* – significance of the difference between the paired means of F and C plots (* $P < 0.05$, ** $P < 0.01$).

Parameter		F ₁	F ₂	C ₁	C ₂	<i>t</i>
Bryophytes	mean no. of species per sample plot	8	8	5	4	**
	no. of species pooled	14	15	6	7	**
	cover (%)	45	55	55	65	*
Vascular plants	no. of species pooled	46	64	72	68	*
	cover (%)	90	85	65	70	**
	aboveground biomass (g/m ²)	260	180	170	154	**

species is characteristic. There are also many species inhabiting tree trunks. Epixylic species are scarcer due to the lack of suitable substrata (decaying wood, stumps) in the seminatural area. Bryophytes inhabiting stones are represented by a smaller group. According to the List of Estonian Bryophytes (Ingerpuu et al. 1994) the following species found on Laelatu meadow are “relatively rare” in Estonia (up to 20 localities): *Frullania dilatata*, *Mnium stellare*, *Thuidium tamariscinum*, *Campylium polygamum*, *Scleropodium purum*, *Encalypta vulgaris* and *Antitrichia curtipendula*. *Antitrichia curtipendula* and *Aulacomnium androgynum* are distributed only in the western part of Estonia. No “rare” bryophyte species (less than 8 localities in Estonia) were found in Laelatu wooded meadow, although there are a remarkable number of rare vascular plants (Krall & Pork 1970). This could be explained by the absence of some habitats that are suitable for many Estonian rare bryophyte species (shady virgin forests, alvars, spring mires), or in other words, a wooded meadow (despite now being rare itself) does not provide rare microhabitats.

The species composition and density at Laelatu show a similarity to those in similar meadows in Western Europe (e.g., Rijnberk & During 1990). 4–10 bryophyte species were counted in 1 m² plots on Laelatu meadow. The number of species counted on several bog plots (4–10 m² in size) was 2–19 (Kask 1965). Hence the species richness seems to be higher on meadow plots. It is also higher than in Estonian forests: 2–7 species per 1 m² in Vilsandi pine forest (Ratas et al. 1993a). The number of epigeic bryophytes in the deciduous forests of Öland on 1 m² plots was 4–12 (Sjögren 1964). The Vilsandi alvar meadow has 10–14 species per 1 m² plot (Ratas et al. 1993b). The number on species-rich Dutch chalk grasslands, 6–12 species as a mean in 1 × 1 m plots (Tooren et al. 1990; During & Willems 1986), is comparable to the number found

in Laelatu meadow. We also noticed the similarity in species composition of Laelatu’s bryophyte vegetation to that of Strelets meadow steppe (Utehin 1965).

Models which are developed in order to explain the mechanisms of species co-existence often view a plant community as a closed system in relation to species composition within a time period of about a decade (e.g., Tilman 1988). According to the view of the community as an open system, the absolute number of species in a plot is the result of a balance between immigration from the species pool and extinction. In our study, the number of bryophyte species in the 1 × 1 m plots (for the mean 50% of the plots) has been found to be in the range 23–34% of their number in the whole set of plots (from the 0.12 ha area), the latter representing 22% of the whole list of Laelatu bryophytes. The respective figures for vascular plant species in plots of the same size are 30–50%, and 25%. Consequently, although a tendency towards a higher concentration of phanerogam species in smaller plots could be noticed, we cannot detect any remarkable difference in the relationships of bryophyte and vascular plant communities to their species pools. The species pool as an important factor which determines the small-scale species richness requires much more attention in bryophyte communities. Until now, the relationship between species number in small plots and their species pools has mainly been investigated for vascular plant communities (Pärtel et al. 1996).

A decrease in the moss cover together with an increase in the cover of the herb layer, caused by fertilisation, as shown by our data, is a well known pattern (Mickiewicz 1976; Brown 1982). Our study shows that the number of bryophyte species increases as the abundance decreases. We recorded no bryophyte species specific to calcicolous semi-natural meadow communities with a rich herb layer (cf., Table 3). After the changes in these communities, including dimin-

ished bryophyte cover as a result of fertilisation and increased herb biomass (still evident 14 years after the last fertiliser application), a series of new bryophyte species immigrated to the plots.

A possible explanation of these results has been derived from the observation that in both layers (bryophyte and herb communities), more species are found in conditions of lower cover or layer biomass. According to the general unimodal species-biomass curve of Grime (1977), species richness increases with decreasing community biomass, up to the rather low value of community biomass corresponding to the maximum diversity. The opposite behaviour of herb and bryophyte layer biomass should consequently lead to contrariwise trends in species richness, as observed in our experiment. The assumption used in this explanation (the independent behaviour of different layers) is supported by the results of Kull et al. (1995) which showed that different layers are well separated by their nitrogen-use-efficiency (which is considerably higher in bryophytes than in herbs).

A different explanation, partly supporting the previous one, comes from the findings of an experiment which showed that the species richness of bryophyte communities increases as a result of fertiliser application together with complete or partial removal of competing phanerogams (Brown 1982). It means that more species can grow on a more fertile soil if this effect is not suppressed by competition.

A comparison of our recent data with the results of the study made more than 30 years earlier (in 1962–63) of the same plots shows a great similarity and only minor changes in the bryophyte community throughout this period. The overall number of bryophyte species found in 1995 (21) is close to that found in 1962–63 (19) (Kalda & Kannukene 1966) on the same plots. The dominant species, *Rhytidiadelphus triquetrus* and *Scleropodium purum*, are the same as in 1962–63. Some species formerly found were not recorded in the plots in 1995: e.g., *Thuidium philibertii*, *Ctenidium molluscum*, but this may be due to the low frequency of these species. The cover values in 1962–63 for vascular plants (F plots – 80, C plots – 65) and bryophytes (F plots – 35, C plots – 50) are close to those described in 1995 (Table 4). Thus, we could not detect any significant changes in the bryophyte community of this site during the last three decades, in contrast to Dutch chalk grasslands which have been strongly impoverished (Tooren et al. 1990). This is probably due to continued traditional management in Laelatu wooded meadow.

The phanerogam community in Laelatu wooded meadow showed a relatively quick response to fertilisation during the first 5–7 years of the experiment in both biomass and species composition, and a very long reversion time (especially concerning species composition and to a lesser extent biomass) after the cessation of fertilizer application, which has also been demonstrated by similar experiments elsewhere (Olf & Bakker 1991). However, the recovery has been considerably slower in our experiment than that reported in some other studies (Mountford et al. 1996; Willems & Nieuwstadt 1996). Bryophytes also exhibited a quick response to fertilisation (Kalda & Kannukene 1966), and a slow recovery of the bryophyte community composition is implied by the present study.

Tooren et al. (1990) showed in experiments on Dutch chalk grasslands that fertilisation had only a minor effect on bryophytes at moderate fertilization levels. Dirkse & Martakis (1992) described a significant rise in the abundance of several bryophyte species as a result of forest fertilisation. Brown & Bates (1990) reached the conclusion that fertilizer additions often reduce bryophyte biomass by the overgrowth of other plants, but when this problem is avoided, fertilizers frequently fail to change the bryophyte cover.

Several papers show the species specificity of responses to fertilizers (e.g., Mickiewicz 1976; Lambert et al. 1986). The most sensitive appears to be forest species (Kellner & Marshagen 1991; Gerhardt & Kellner 1986). In a forest fertilization experiment, *Hylocomium splendens* and *Pleurozium schreberi* declined strongly at nitrogen doses of over 3 g m⁻² per year (Dirkse & Martakis 1992). This data fits well with the results of Kalda and Kannukene (1966) who also found that the first species to disappear in response to fertilizing were *Hylocomium splendens* and *Pleurozium schreberi* and the most tolerant species was *Rhytidiadelphus squarrosus*. This tendency corresponds with the results of the present study (Table 2). The preference for more fertile sites may also explain the distribution pattern of *Rhytidiadelphus squarrosus*, which was sparse in the meadow in 1995, growing almost only on the experimental plots, and mainly on the plots previously fertilised.

A problem which should not be overlooked when comparing the dynamics of diversity in vascular plants and bryophytes, is the possible direct interaction between these two plant groups in communities. One aspect of these interactions is the role of bryophytes in phanerogams' recruitment from seed. According to the study by Krall & Pork (1970) from the same Laelatu

area, the C plots with more extensive bryophyte cover have a lower seedling frequency than the F plots, but a higher frequency of species having mycotrophic juveniles. This may be a result of shading provided by bryophytes and the chemical compounds derived from them. It has been shown (Tooren 1990; Hein 1966) that mosses may decrease herb germination. Herbs with large and nutrient-rich seeds, as well as bacteriotrophic, mycotrophic or hemiparasitic herbs, are more tolerant to bryophyte cover. In this way, bryophytes could have a certain role in the functioning of the species-rich meadow community. By diminishing the generative reproduction of dominant phanerogam species and increasing a chance for mutualistic relationships (During & Tooren 1990), they could give some less-frequent species a greater opportunity to co-exist. However, these effects are probably not very strong, since vegetative reproduction plays a major role in these communities.

Conclusions

The epigeic bryophyte flora on Laelatu wooded meadow is relatively rich in species. It is characterised by the occurrence of several calciphilous species. Vascular plants and bryophytes respond in opposite ways to fertilisation – it increases the coverage and diminishes the number of species in vascular plants, but diminishes coverage and increases the number of species in bryophytes. The relationship between the number of species in a small plot and the number of species in the species pool of the same area is similar for both vascular plants and bryophytes. No significant changes in the bryophyte community could be detected in Laelatu wooded meadow during the last three decades.

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