

Impact of Phanerogam and Soil Characteristics on Bryophyte Assemblages with Respect to Restoration Practices (Case Study: IJzermonding, Belgium)

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ABSTRACT The effect of soil and phanerogam characteristics on bryophytes composition, richness, abundance and functional groups were investigated in order to understand the factors responsible for bryophytes distribution patterns. Three different sand dunes were selected: untouched, artificial sod-covered and planted by *Ammophila*. Along 10 transects perpendicular to the shore, a total of 142 permanent relevés, located in three sand dunes, were sampled. In each plot, total cover of vascular herbaceous and bryophytes, and the percentage of litter were estimated. The average of vascular herbaceous height was measured. In each plot, EC, pH, CaCo₃, texture and organic matter content of the upper 5 cm layer were also measured. Analyses using DCA and GLM showed that bryophytes abundance was decreased by EC and phanerogam abundance, while pH increased the species richness of bryophytes. EC increased the relative abundance of sexual species while decreased the relative abundance of asexual bryophytes species. The relative abundance of colonists increased in planted *Ammophila* sand dune while the relative abundance of perennial stayers was the highest in untouched sand dune. The successional stage should also be important in distribution pattern of bryophytes.

Key words: Bryophyte, Phanerogam cover, Sand dune, Soil characteristics, Restoration management, Succession

1 INTRODUCTION

Explaining observed patterns in species diversity over space is a fundamental goal of plant ecology (Mill and Macdonalds, 2004). Understanding the most important factors driving distribution patterns of plant communities can constitute a tool for vegetation management and conservation (Mueller-Dombois and Ellenberg, 2002). Bryophytes

play an important role in the structure and function of plant communities, especially if they reach a high cover (van Tooren *et al.*, 1990). A dense cover of bryophytes prevents water evaporation from the soil surface (Stoutjesdijk and Barkman 1992), increase habitat heterogeneity (Rundel 1978) and productivity of phanerogams (Rieley *et al.*, 1979, Crittenden 1983). Nevertheless, bryophytes have

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received relatively little attention in compare with phanerogams to be studied on their relationships with environmental condition, probably because of their cryptic nature and small size (Mills and Macdonald 2004).

Many biotic and abiotic factors can affect on species composition and distribution of bryophytes including phanerogams. The phanerogams determine the microclimate of cryptogams (Martinez-Sanchez *et al.*, 1994) and their nutrient availability (During and Verschuren 1998). Vascular plants could facilitate bryophytes and the cover of some bryophytes species increased with increasing percentage cover of vascular plant, because this creates a better microclimate, e.g. optimized temperature (Ingerpuu *et al.*, 2005). While in other cases, it has been repeatedly reported that total cover of phanerogams decreased total cover of bryophytes (Zamfir *et al.*, 1999; Bergamini *et al.*, 2001; Ejrnæs and Poulsen 2001) and bryophytes were only common under a sparse upper layer and were light-limited through vascular plant cover (Kull *et al.*, 1995). As a result, the impact of phanerogams on bryophytes has frequently been investigated in the past but conclusions are often contradictory, feeling to need more study on this subject.

In addition, soil condition can also affect diversity, distribution, composition and survival of bryophytes. The occurrence and abundance of some bryophytes species is be found to be determined by the presence of a specific substrate and soil (Watson 1980; Kimmerer 1993; Vitt *et al.*, 1995; Martinez and Maun 1999). It was reported that soil condition was the most important factors affected and predicted bryophytes species distribution. For instance, some species exhibited an increasing probability of occurrence with being the loamy-sandy soils. It was also concluded that some species were only found in forest habitat because of the presence of acidic habitats and the higher soil moisture content. In addition, the

occurrence of some bryophytes species could be significantly predicted from the presence of pebbly soils cover with pH ranging between 6 and 9 (Dull 1992). Therefore, it can be expected that soil conditions and characteristics of the phanerogame community will determine the species composition and pattern of bryophytes in sand dune habitat.

Our objectives were to assess the effect of (i) characteristics of the phanerogam layer (phanerogam cover and height) and (ii) soil factors (litter percentage, pH, EC, texture, organic matter content and CaCo₃) on species composition, richness, and abundance and functional groups of the bryophytes layer. Because study area was restored through some kind of restoration projects in which some parts covered with natural sods, some parts planted with Marram grass and some parts remain untouched, we also considered (iii) the relationship between the kinds of restoration treatments with the abundance of different species of bryophytes.

2 MATERIALS AND METHODS

2.1 Study area

The study area is part of the Flemish Nature Reserve De IJzermonding, which is situated along the Belgian coastline. It concerns the sand dune part of the nature reserve, which borders the intertidal estuary area along the river bank. The area underwent large-scale restoration measures in the intertidal-supratidal salt marsh-sand dune ecotone; the sand dune area itself was largely untouched. To protect the hinterland for flooding, several sand dikes were created, some of which were planted with *Ammophila arenaria* while others were covered with natural sods from other dune area in 2001. Sand dunes are therefore differentiated in recently created Marram dune with *Ammophila* dominance, recently sod-covered sand dunes with low grass dominance, and untouched sand dunes with high pleurocarpous cover up to

untouched sand dunes with moss dominance. The high variation in vascular plant composition and soil characteristic was created substantial spatial heterogeneity in the study area.

2.2 Data collection

The study area was divided into three habitats according to the kind of restoration management. Along 10 transects, perpendicular to the shore, a total of 142 permanent relevés (each 2*2m) were established with 3 meters distance in between. 15 plots were located in sod-covered dune, 77 plots were located in intact dune (hereafter called 'no-restoration' dune) and 50 plots were located in Marram dune.

The cover of all occurring vascular herbaceous species and bryophytes were estimated in each plot using the decimal Londo-scale (Londo, 1976). Samples were taken in July and September in 2005.

Additionally, Plant height was measured by meter in many plots and was estimated in others according to the measured plots. The bryophyte specimens were collected to be identified in the laboratory.

In each plot, soil samples were also collected in upper 5 cm and carried to the laboratory for texture and chemical analyses. Analysis of soil texture, EC and organic matter content was executed in the laboratory. After shaking 5 grams of soil in 50 mm distilled water for two hours, the electric conductivity (EC) was measured with a WTW Inolab EC meter level 1 and pH with pH meter. Organic matter content was measured after ignition of soil samples at 550 °C and CaCo₃ at 900 °C. Soil texture was determined with a Coulter LS Particle Size Analyzer. As soil texture characteristic, we used the median particle size (D₅₀) (Erfanzadeh *et al.*, 2010).

2.3 Functional types

The selection of functional types was based on previous studies (During 1979, Kürschner 2004,

Söderström and Gunnarsson 2003) and prior expectations about possible relationships with the phanerogam characteristics and soil factors. Two groups (colonists and perennial stayers) were determined, comparing the contribution of each species to the life strategy. Three groups (sexual, asexual and sexual-asexual) were determined, comparing the contribution of each species to the productive strategy (Siebel and During, 2006). For each functional type, we calculated the relative abundance of each category value in every plot, by summing the cover data of all species with that functional type, and dividing it by the sum of the cover of all categorized species in the plot.

2.4 Data Analysis

Bryophytes community composition was assessed by detrended correspondence analysis (DCA), using CANOCO (Lepš and Šmilauer 1998). Since axes 1 and 2 explained a large proportion of the variation (table 1), only scores on the first two axes were used as a measured for bryophytes species composition.

Among EC, organic matter content and CaCo₃ strong intercorrelations were presence, therefore, we retained EC and ignored organic matter content and CaCo₃. In addition, we ignored litter percentage because of strong intercorrelation with herbaceous height. A general linear model was used to study the effect of soil and phanerogam characteristics on bryophytes functional groups, total cover, richness and composition. Restoration managements were introduced into the model as fixed factor (three categories), soil and phanerogam characteristics and their interactions with restoration management as covariates. A LSD test was used to evaluate the significantly differences among restoration managements.

Table 1 The mean \pm SE of ground cover and herbaceous height in restoration treatments.

Restoration treatment	Herbaceous height (cm)	Litter (%)	Dominant vascular plant	Dominant bryophyte species
Intact area	22.9 \pm 1.4	10.9 \pm 0.1	<i>Festuca rubra</i>	<i>Homalothecium lutescens</i>
Sod covered	20.7 \pm 3.1	11.0 \pm 2.4	<i>Festuca rubra</i>	<i>Homalothecium lutescens</i>
Maram planted	76.7 \pm 3.3	16.5 \pm 1.0	<i>Ammophyla arenaria</i>	<i>Tortula ruralis</i> var. <i>ruraliformis</i>

3 RESULTS

3.1 Effect of environmental variation on species composition

The vascular plant cover varies from very dense to very scarce, vegetation height varies substantially too in the study area. Field survey showed that dominant vascular plant and bryophyte species in three kinds of restoration treatments are different (table 1). Table 1 and 2 show also some more details about soil and ground cover of different restoration treatments. The most abundant bryophytes species in all three kind managements were: *Barbula convulata*, *Barbula unguilata*, *Brachythecium albicans*, *Brachythecium rutabulum*, *Bryum argenteum*, *Bryum bicolor*, *Bryum cappilare*, *Cladonia furcata*, *Cladonia pxicata*, *Eurhynchium praelongum*, *Homalothecium lutescens*, *Hypnum cupressiform*, *Leptobrium pyriforme*, *Pseudoscleropodium purum*, *Rhychostrichum megapolitanum*, *Tortula ruralis* var. *ruraliformis*.

The first two DCA axes explained about 13.5 and 11.3% of the total species variability, respectively (table 3). DCA1 was significantly correlated with herbaceous

height while DCA2 was significantly correlated with the herbaceous cover and restoration managements (table 4).

3.2 Relationship between environmental variables and bryophytes cover and richness

EC, pH and restoration managements and interaction between restoration managements and herbaceous cover (table 4) significantly affected bryophyte species richness. Bryophytes richness was increased ($b=0.46$, $t= 2.12$, $p<0.05$) with increasing pH and decreasing EC ($b=-0.007$, $t= -2.01$, $p<0.05$).

The GLM analysis showed that the average richness in no-restoration plots is significantly less than sod-covered and Maram plots (0.42 m² versus 0.55 m² and 0.53 m²). There was no significant differences between sod-covered and Maram plots in species richness.

Total cover of bryophytes was significantly affected by EC and herbaceous cover (table 4). There was negative correlation between total cover of bryophytes with EC ($b=-2.2$, $t=-2.33$, $p<0.05$) and herbaceous cover ($b=-0.47$, $t=-2.00$, $p<0.05$) (Figure 1).

Table 2 The mean \pm SE of soil factors in restoration treatments.

Restoration treatment	EC (μ s/cm)	pH	Organic matter (%)	CaCo3 (%)	Texture (μ m)
Intact area	118 \pm 3.5	7.9 \pm 0.2	2.8 \pm 0.2	5.0 \pm 0.2	219 \pm 3.4
Sod covered	122 \pm 4.2	8.1 \pm 0.3	2.4 \pm 0.1	4.9 \pm 0.1	220 \pm 1.2
Maram planted	114 \pm 1.7	7.9 \pm 0.4	1.7 \pm 0.1	4.8 \pm 0.1	223 \pm 1.0

Table 3 Eigenvalues for DCA axes and correlation between axes and species-environment.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.89	0.62	0.41	0.21	6.64
length of gradients	5.75	4.80	3.69	3.76	
Cumulative percentage variance of species data	13.5	24.8	29.00	32.10	

Table 4 Result of the general linear model analysis for composition, total cover, richness and functional groups. Only significant responses are shown.

Dependent variables	Independent variables	Mean square	F-statistic	P-value
AX1	Herbaceous height(cm)	6.61	11.76	0.001
AX2	Restoration management	1.74	3.6	0.03
	Herbaceous cover(%)	5.96	12.4	0.001
Total cover of bryophytes	Restoration management	4733.88	7.88	0.001
	EC	3022.29	5.43	0.021
	Herbaceous cover*restoration	2825.01	5.08	0.007
	Herbaceous cover (%)	3368.67	6.06	0.015
Bryophytes species richness	Restoration management	4.65	5.9	0.003
	EC	3.2	4.06	0.046
	pH	3.7	4.4	0.037
	Restoration * Herbaceous cover	2.47	3.1	0.027
Relative abundace of colonist	Herbaceous height(cm)	0.61	16.17	0
	pH	0.26	7	0
	Restoration management	0.71	16.66	0
Relative abundance of perennial stayers	Herbaceous height(cm)	0.61	16.17	0
	pH	0.26	7	0
	Restoration management	0.71	16.66	0
Relative abundance of sexual	EC	0.45	3.8	0.05
	Herbaceous height(cm)	0.16	7.53	0.007
Relative abundance of asexual	pH	0.09	4.7	0.032
	Herbaceous height(cm)	0.17	8.37	0.004
Relative abundance of sexual-asexual	Restoration management	0.52	5.7	0.004
	Herbaceous cover(%)	0.75	8.1	0.005

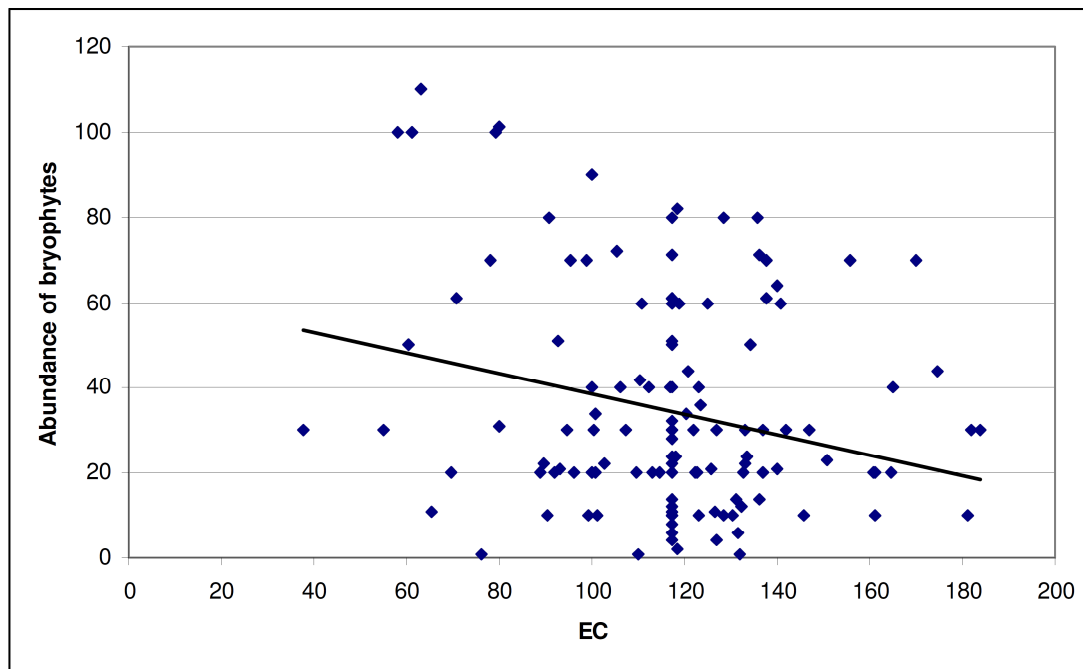


Figure 1 Bryophytes abundance (%) in relation with EC.

3.3 Relation between environmental variables and bryophyte functional groups

Herbaceous height, pH and restoration management affected the relative abundance of colonists and perennial stayers (table 4). Relative abundance of colonists increased with herbaceous height ($b=0.004$, $t=4.02$, $p<0.01$) and pH ($b=0.13$ and $t=2.64$, $p<0.01$). In contrast, the relative abundance of perennial stayers decreased with herbaceous height ($b=-0.004$, $t=-4.02$, $p<0.01$) and pH ($b=-0.13$ and $t=-2.64$, $p<0.01$). LSD revealed that the relative abundance of perennial stayers and colonists were different among restoration management with highest of colonists in Marram plots and highest perennial stayers in no-restoration plots ($F=16.66$ and $p<0.01$). There was no significantly difference between sod- covered plots with Marram plots and no-restoration plots for relative abundance of colonists and perennial stayers.

The relative abundance of sexual species was significantly affected by EC and herbaceous height while the relative abundance of asexual species was affected by pH and herbaceous height. Restoration management and herbaceous cover significantly affected the relative abundance of sexual-asexual species (table 4). Sexual species increased with EC ($b=0.07$, $t=1.97$, $p<0.05$) and height ($b=0.002$, $t=2.7$, $p<0.01$). Asexual species was increased with pH ($b=0.08$, $t=2.16$, $p<0.05$) and height ($b=0.002$, $t=2.89$, $p<0.01$). Sexual-asexual species was affected by herbaceous cover. It decreased with increasing herbaceous cover ($b=-0.006$ and $t=-3.33$, $p<0.01$).

4 DISCUSSION

In this study, it was considered restoration managements as an environmental factor and introduced to the model like other environmental factors (e.g. EC). However high correlation between DCAs as a proxy of

bryophytes composition with phanerogam height and cover, it seems that phanerogam characteristics have more effect on spatial distribution of bryophytes composition than soil characteristics. The high correlation (negative or positive) between bryophyte composition and phanerogam composition has already been shown in some temperate grassland (During and Lloret 1996, Zamfir *et al.*, 1999). Nevertheless, we think that the spatial change in bryophytes composition also is a respond to the kind of restoration management and the succession stages. Marram plots mostly were characterized by colonists, while in no-restoration plots perennial stayers were most abundant. If we accept that no-restoration plots were in late successional stages and Marram plots in early successional stages (Packham and Willis 1997), it could be possible to appear some particular bryophytes in each restoration management in relation to their successional stages. The colonists often appear early in secondary succession series, together with or shortly after the fugitives (Joenje and During 1977). Having small spores less than 20 μm and long distance dispersed might help colonists to establish in newly created Marram more than other life strategies. In contrast, in no-restoration plots, perennial stayers species had more relative abundance than colonists. These results confirm the finding of During (1979), that perennial stayers fit in more or less constant environment, or such, which may last very long.

Total cover (abundance) of bryophytes was the second characteristic which considered in this study. Bryophyte abundance decreased with increasing phanerogam abundance. The competition between phanerogams and bryophytes might be the cause of negative correlation between phanerogams and bryophytes abundance (Zamfir *et al.*, 1999). Established phanerogams can theoretically influence bryophytes negatively. A negative

effect is the reduction of light availability (Ingerpuu *et al.*, 2005) particularly for acrocarpous mosses in sunny, dry and xeric habitats (Kürschner 2004). In our case, competition for space might be more important. In fact, most bryophytes species in sand dunes are poor competitors and are suppressed by excessive vascular plant growth (Siebel and During 2006). Biomass and cover of bryophytes and vascular plants has been found to be negatively correlated in some other studies as well (Ingerpuu *et al.*, 1998; Bergamini *et al.*, 2001).

Bryophyte abundance decreased also with increasing EC. Most species in the study area are sensitive to salinity (Siebel and During 2006), which might affect the total cover of bryophytes. Nevertheless, EC was positively correlated with the cover of sexual species in our study area. Being some salt tolerance species in this group might explain the increasing of sexual species with EC such as *Bryum* ssp. Previous study also showed that the genus of *Bryum* can sometimes be found in upper salt marsh on bare ground, particularly on the ecoton between dune and marsh where the soils are sandy and saline. In addition, *Bryum capillare* were found the most common bryophytes in the high intertidal of salt marsh with high degree of salinity (Garbary *et al.*, 2008).

The variation of pH among restoration managements was not too much (see table 1: a range of 7.9-8.1). Nevertheless, functional groups and richness of bryophytes was significantly affected by soil acidity. In previous study the heterogeneity of edaphic factors among sites was high and then was stated that pH could be an important factor influenced bryophytes layer. Zamfir *et al.* (1999) found that pH affected bryophytes species distribution in grassland habitat.

Bryophytes richness was higher in Marram dune than no-restoration dune. Being of

colonists, which related in early successional stages, with together most species related to late successional stage i.e. *Brachythecium rutabulum*, *Homalothecium lutescens*, *Hypnum cupressiforme*, *Pseudoscleropodium purum* increased the species richness in Marram dune. These species had appeared in Marram dune, although in very low abundance, probably because of shade and leaching effects of the grass, which may have favored these perennial stayers (During 1988). In contrast, in stable no-restoration plots colonists were absent or rare, which decreased their species richness.

We showed that pH could increase bryophyte species richness, which is accordance with previous studies (Mill and Macdonalds, 2004; Hylander and Dynesius, 2006; Virtanen *et al.*, 2000).

5 CONCLUSION

Restoration management was the most important environmental factor which significantly affected on most bryophytes characteristic such as composition, total cover, functional group and richness. It can be concluded that restoration management determined the successional stages and then successional stages affected the kind of soil and phanerogam characteristics and finally soil and phanerogam characteristics impacted the cryptogam layer. One might expect that in Marram dune, perennial stayers should be dominant in bryophytes layers because of more herbaceous height, which could increase leaching and shade appropriate for perennial stayers. But in this study, colonists which usually appear in sunny and dry places, are dominant in Marram dune. Perhaps, Marram dune was dominated by colonists because of their lower age (early successional stages) in this restoration management.

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تأثیر خصوصیات خاک و گیاهان آوندی بر پوشش خزهایها در ارتباط با عملیاتهای مختلف اصلاحی (مطالعه موردی: آیزرموندینگ، بلژیک)

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چکیده در این تحقیق تأثیر خصوصیات مختلف خاک و گیاهان آوندی بر ترکیب، غنا، فراوانی و گروههای عملکردی خزهایها به منظور فهم بهتر عوامل مؤثر بر پراکنش آنها مورد مطالعه قرار گرفت. بدین منظور سه منطقه ماسه‌زار که از لحاظ فعالیت‌های اصلاحی متفاوت بودند انتخاب شدند شامل: پوشانده شده با چمن مصنوعی، کاشت شده با گیاه *Ammophila* و منطقه دست نخورده. داده‌های خاک و پوشش از ۱۴۲ پلات ۴ مترمربعی که در طول ۱۰ ترانسکت عمود بر خط ساحلی مستقر شده بودند، برداشت شدند. در هر پلات پوشش کل گیاهان آوندی، خزهایها و درصد لاشبرگ تخمین‌زده شدند. همچنین در هر پلات، EC، pH، CaCO_3 ، بافت و مواد آلی خاک سطحی (تا عمق ۵ سانتی‌متر) اندازه‌گیری شدند. سپس داده‌ها توسط GLM و DCA آنالیز گردیدند. نتایج نشان داد که فراوانی خزهایها با افزایش EC و فراوانی گیاهان آوندی کاهش می‌یابد. همچنین غنای گونه‌های خزهایها با pH رابطه مستقیم دارد. EC باعث افزایش فراوانی گروه عملکردی خزهایهای جنسی و کاهش خزهایهای غیرجنسی شد. تجمع گراها در منطقه‌ای که با *Ammophila* کاشت شده بود بیشترین فراوانی را داشتند در حالی که گونه‌های دائمی در منطقه دست نخورده بیشترین فراوانی را داشتند. این تحقیق نشان داد که مراحل جانمایی در الگوی پراکنش خزهایها مهم می‌باشد.

کلمات کلیدی: پوشش گیاهان آوندی، تپه‌های ماسه‌ای، توالی پوشش، خزهایها، عوامل خاکی، مدیریت احیاء