GREY DUNE GROUND LAYER VEGETATION IN THE CURONIAN SPIT NATURE RESERVE, LITHUANIA

РАСТИТЕЛЬНОСТЬ СЕРЫХ ДЮН ЗАПОВЕДНИКА "КУРШСКАЯ КОСА" В ЛИТВЕ

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Abstract

Structural composition of the ground layer vegetation on sandy dunes of the Curonian Spit Nature Reserve, Lithuania, is described. The Curonian Spit is a 98 km long, narrow sandy ridge at the eastern coast of the Baltic Sea, belonging partly to Lithuania and partly to Kaliningrad Province of Russia. The ground layer vegetation structural elements include lichens and bryophytes, with vascular plants representing the field layer. Along the vegetation succession on the grey dunes, the vascular plants dominating in the early stages are substituted by bryophytes and lichens. The bryophytes become dominant towards the late stages of the succession of the ground layer communities. The role of species interactions as regulators of the ground layer vegetation is discussed.

Резюме

Описана структура растительного покрова, и в первую очередь мохов-лишайникового яруса, дюн природного заповедника "Куршская коса" в Литве. Куршская коса простирается на 98 км, представляя собой узкий песчаный гребень в восточной части Балтийского моря, находящийся отчасти на территории Литвы, отчасти в России. Рассматриваются стадии сукцессии, происходящие не уровне мохово-лишайникового покрова, во процессе которых сосудистые растения, поселяющиеся на дюнах первыми, постепенно вытесняются густым мохово-лишайниковым покровом. Мохообразные становятся доминантами на поздних стадиях этой сукцессии. Обсуждаются взаимоотношения и роль некоторых видов яруса мохообразных.

KEYWORDS: bryophytes, lichens, vascular plants, dunes, vegetation structural elements

INTRODUCTION

The Curonian Spit is a 98 km long, narrow sandy ridge between the Curonian Lagoon and the Baltic Sea on the western coast of Lithuania and Kaliningrad Province of Russia (Fig. 1). The Spit was originally forested, but along the history trees have been cut and the bare moving sand has formed high dunes by mainly westerly and south-westerly winds from the Baltic Sea. The vegetation on dunes consists of relatively drought-tolerant species with adaptations to hot exposed habitats and tolerance of moving sand. The Curonian Spit dunes are recognized as a distinct geographical vegetation unit, and the villages and nature reserves are nominated as a Unesco World Heritage Site.

The dynamics of the vegetation on moving sand dunes have been previously studied *e.g.* by Steffen (1931), Bandžiuliene (1977), Stankevičiūtė (2000a, 2000b, 2006) and Peyrat (2010). The successive stages and vascular plant species composition of white and grey dunes are relatively well-known. The bryophyte and lichen flora and communities of the Curonian Spit have received less interest, even though species occurrences are mentioned in many of the studies on dune vegetation (*e.g.*, Bandžiuliene, 1977; Stankevičiūtė, 2000a, 2000b, 2006, and Peyrat, 2010). The liverworts of the Russian part of the Curonian Spit have been investigated by Dolnik & Napreenko (2007) and a list of liverwort species observed in the Lithuanian part of the Spit is published by Kalinauskaitė & Laaka-Lindberg (2012).

The sand dune vegetation is divided in two major types, white dunes and grey dunes (see *e.g.* Stankevičiūtė, 2000a, 2006). On white dunes the vegetation is dominated by vascular plants with high tolerance of moving sand and barely no ground layer present. Grey dunes are gradually formed of the white dunes by getting more stable as the plant cover increases and ground layer slows the sand movement. In the Lithuanian part of the Spit, the white dunes of the Curonian Spit Nature Reserve form approximately 60% of the total area of moving sand, while grey dunes cover about 40%. However, the transition from white to grey dunes via the early successional stages of the dune vegetation is more or less indistinct.

The sparse vegetation cover on white dunes consists mainly of patchily distributed grasses and *Salix* on dune

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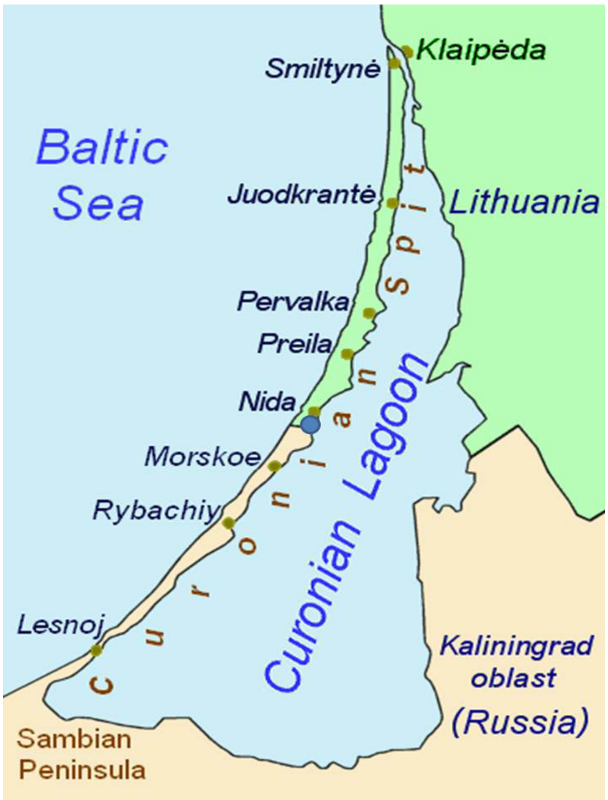

Fig. 1. Location of the Curonian Spit and the study area in the Curonian Spit Nature Reserve, Nida, Lithuania, in the eastern coast of the Baltic Sea (source of the map: http://en.wikipedia.org/wiki/Curonian_Spit).

tops (Stankevičiūtė, 2000a), while on the grey dunes it forms a mosaic of different associations mostly depending on the location on dune slopes and on dune age. On young dunes and on more exposed slopes the vegetation cover is low, and species composition less diverse than on older dunes, on which the vegetation stabilization has proceeded and tree seedlings, mainly pines (*Pinus sylvestris*) and willows (*Salix* spp.), start to appear. The overall plant diversity and cover increases with the succession (see Stankevičiūtė, 2000a).

Our study concentrates on yet un-forested grey dunes as on the basis of the previous observations (*e.g.* by Kalinauskaitė & Laaka-Lindberg, 2012), the ground layer does not exist on un-stabilized white dunes. Obviously the starting point for dune stabilization and vegetation succession is the establishment of grasses on ridges of white dunes. Very soon on the open side of the moving dunes establishment of plants becomes possible and bryophytes and lichens favoring open habitats gradually take over and the sand movement slows down. This facilitates additional species establishment. The vascular plant facilitation on bryophyte establishment in open grassland vegetation has been demonstrated by Ingerpuu *et al*. (2005). Increasing ground layer cover increases soil water-holding capacity and thereafter facilitates vascular plant seed germination and seedling establishment, which, however, differs between species (Keizer *et al*., 1985; Zamfir, 2000). Gradually, as the plant cover begins to settle the ground layer species including terrestrial macro-lichens and bryophytes take over, stabilize the sand and initiate the vegetation development towards pine-dominated forests (see Stankevičiūtė, 2000b).

In this study, we describe the composition of ground layer vegetation and compare the differences in the proportions of vegetation structural elements among clusters of plots sampled on grey dunes in Curonian Spit Nature Reserve. On the basis of our results we discuss the successional process of the grey dune vegetation with special focus on the role of bryophytes in the dynamics of the grey dune ground layer succession. Our general aim is to direct attention to this rare and fragile vegetation type of the Curonian Spit dunes.

STUDY AREA

The study area is located in southern end of the Lithuanian part of the Spit, in the Curonian Spit Nature Reserve in Nida, Lithuania. Our study in autumn 2011 concentrated on open grey dunes with vegetation type corresponding to the phytosociological class *Koelerio-Corynephoretum* Klika in Klika & Novak (Stankevičiūtė

Table 1. The vascular plant, lichen and bryophyte species recorded on the 0.5x0.5 m sample plots in grey dunes in the Curonian Spit Nature Reserve in Nida, Lithuania in autumn 2011. **Cladonia* spp. includes both un-identified species with horn-like pseudopodia and sterile phyllocladia. Species general abundance on the plots: very scarce = 1, scarce = 2, abundant = 3, very abundant = 4.

Vascular plants	Abundance	Lichens	Abundance	Bryophytes	Abundance
Agropyron dasyanthum	3	*Cetraria ericetorum*	4	Mosses:	
Corynephorus canescens	3	*Cetraria islandica*	3	*Brachythecium albicans*	2
Erigeron acris	2	*Cladonia arbuscula*	4	*Ceratodon purpureus*	4
Festuca polesica	4	*Cladonia mitis*	2	*Climacium dendroides*	1
Festuca rubra	4	*Cladonia spp.**	4	*Dicranum polysetum*	2
Hierachium umbellatum	3			*D. scoparium*	2
Jasione montana	4			*Pohlia nutans*	4
Linaria loeselii	4			*Polytrichum juniperinum*	2
Pilosella officinarum	2			*P. piliferum*	4
Pinus sylvestris	1			*Racomitrium canescens*	3
Rumex acetosella	4			Liverworts:	
Thymus serpyllum	1			*Cephaloziella divaricata*	4
Viola littoralis	1			*C. rubella*	3
Viola tricolor	2				

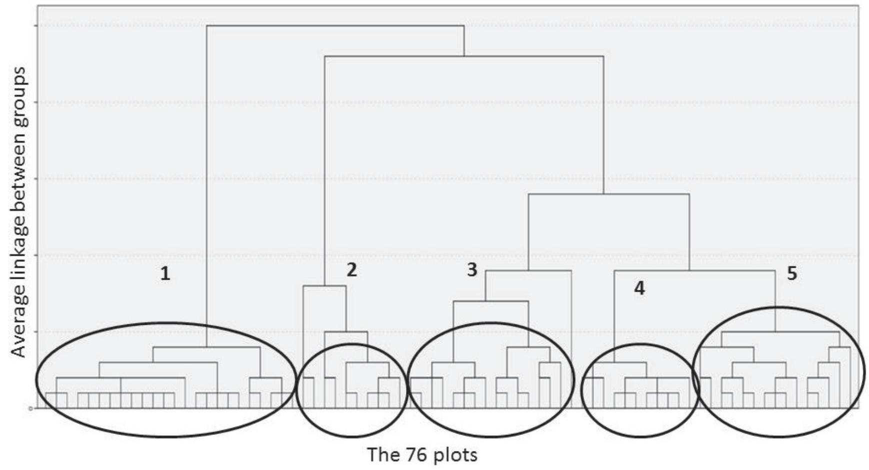

Fig. 2. Dendrogram illustrating the hierarchial cluster analysis of the 76 ground layer vegetation plots on the grey dunes in the Curonian Spit Nature Reserve, Lithuania. The clustering is performed hierarchially on group linkages based on squared Euclidean distances. The numbered clusters 1-5 are indicated by circles.

2000a). The total area of the National Park is about 18.000 ha, and the total area of the sampled part of the reserve is about 200 ha. The vegetation is extremely sensitive to trampling by humans, animals and vehicles, and completely disturbance-free dune surface is scarce.

Material and Methods

We randomly placed 76 plots of 0,5×0,5 m on dune slopes, with at least 10 m between the plots. The maximum distance between the plots is about 1 km. We treat the vegetation as structural elements consisting of field layer with vascular plants, and ground layer with the two elements, bryophytes and lichens treated separately. The vegetation elements are treated as compilations of the species recorded on the plots. One more structural element could be seen, the proportion of the bare sand, but as this is complementary to the total cover of the other elements on the plots, it was not included in the analyses. The total percentage cover of the structural elements is estimated on each plot. The vascular plant, lichen and bryophyte species are listed with observed abundance on plots on scale very scarce = 1, scarce = 2, abundant = 3, very abundant = 4. The exposure of the plot is measured as the compass direction of the dune slope opening towards N, NW, W, SW, S, SE, E and NE. If the plot is on flat surface, the exposure is defined as zero (0). For coding of the exposure measure the directions are given a numerous value clockwise as follows: 3 for E, 6 for S, 9 for W and 12 for N and, with intermediate values for the middle directions NW 10.5, SW 7.5, SE 4.5 and NE 1.5 . In our dataset the variables appear as normally distributed (Kolmogorow-Smirnov test) with homogenic variances.

A cluster analysis is performed on the 76 vegetation plots. A hierarchy clustering is performed on between groups linkage based on squared Euclidean distances (see SPSS – Cluster Analysis 2013). The variables included in the clustering include the total vegetation cover, cover of the structural elements and the exposure of the plots. The proportions of the structural elements were compared between the clusters by one-way ANOVA with Tukey□s *post hoc* test (see *e.g*. Ranta *et al*., 2012) in order to see if the differences in proportions of the structural elements between the clusters are significant. Furthermore, the Pearson correlation test was used to clarify whether the variables are correlated to each other. All statistical tests were computed by PASW® Statistics 18 softwear (see PASW 2013).

The vascular plant nomenclature follows Stankevičiūtė (2000a), lichen names are after Stenroos *et al.,*

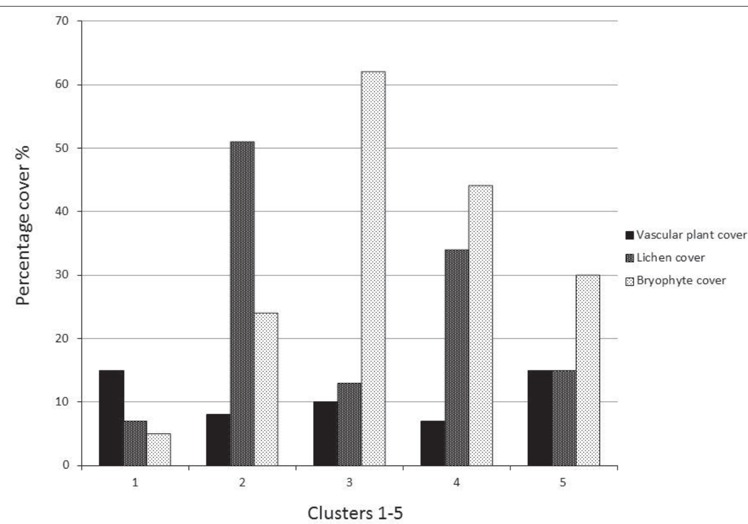

Fig. 3. The percentage cover of the vegetation elements (vascular plants, lichens and bryophytes) in the 5 clusters formed in the hierarchial cluster analysis (see Figure 2) represent different stages along the succession of the grey dune ground layer in the Curonian Spit Nature Reserve, Lithuania.

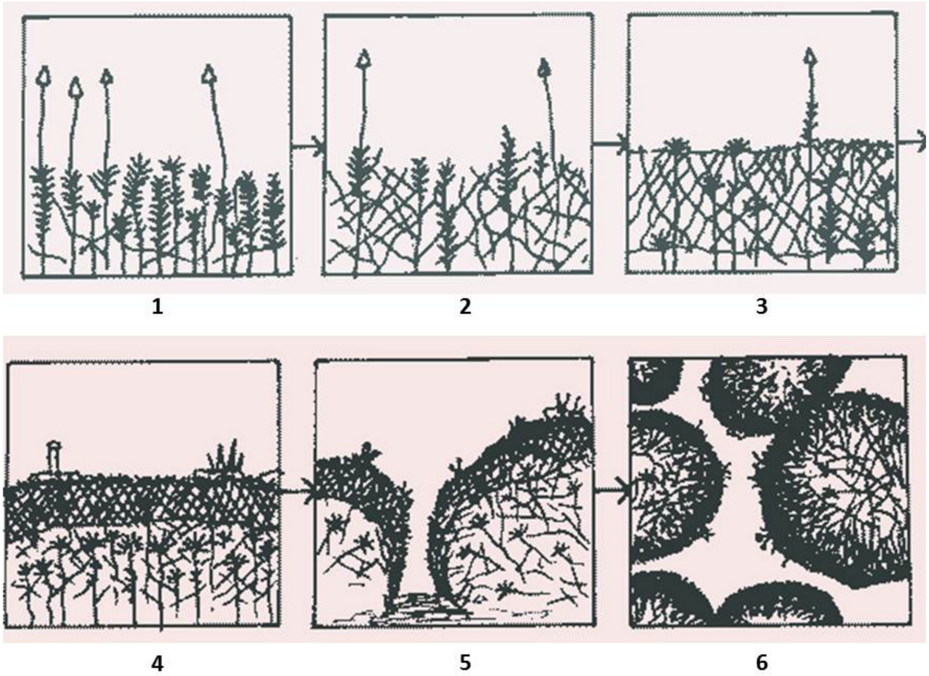

Fig. 4. A schematic view over the successive stages is presented from early stage 1 on the upper left corner to middle stages 2-4, and to late stage 5 on bottom right corner. The numbers 1-5 refer approximately to resulting groups in the cluster analysis. The samples are shown in side view, except for the stage 5 which is shown also from above (6). The most common bryophytes are shown by thin crossing lines for *Cephaloziella divaricata* and the stout upright shoots *Polytrichum piliferum* (some illustrated with sporophytes). In stage 4, the hornlike lichens *Cladonia* spp. are also illustrated.

(2011) and bryophyte names are based on Ulvinen & Syrjänen (2009).

RESULTS

The total number of species recorded and identified on the sample plots is 29. The vascular plants (14 spp.), bryophytes (9 mosses and 2 liverworts) and macro-lichens (4 spp.) found on the grey dune vegetation plots are listed in Table 1. The total number of vascular plant species could not be recorded reliably as the sampling was done in autumn in turn of September and October, when many of the vascular plants had already wilted. On the basis of previous published lists of vascular plants (Stankevičiūtė 2000a), we estimate that only about 10% of the species recorded on the same phytosociological class were found on our plots. The vascular plants with highest abundance (4) on the plots are *Festuca polesica, F. rubra*, *Jasione montana*, *Linaria loeselii* and *Rumex acetosella.* Lichens occurring with highest abundance are *Cetraria ericetorum, Cladonia arbuscula* and several *Cladonia* species treated as a group, as most of them occurred only as phyllocladia and could not be identified on species level in the field. The bryophytes with highest abundance on the plots include the liverwort *Cephaloziella divaricata* and common pioneer mosses *Ceratodon purpureus, Pohlia nutans* and *Polytrichum piliferum*.

The total vegetation cover on the studied grey dune plots varies from 14 % to 99 % on the total of 76 plots. The cluster analysis based on the variables total vegetation cover, percentage cover of the structural elements (vascular plants, lichens and bryophytes) and the exposure of the plots produces 5 clusters corresponding to the four first hierarchy levels of the clustering (Fig. 2). These clusters are interpreted as partly referring to the successional stages of the ground layer vegetation (1 early stage, 2-4 middle stages and 5 late stage). The first cluster is coded as early stage = 1, the intermediate clusters as middle stages = 2, 3 and 4 and the fifth cluster as late stage = 5 (see also Fig. 4).

The average values of the variables among the clusters are compiled in Table 2. The one-way ANOVA shows significant differences in total vegetation cover between the clusters (F = 91.409, p = .000), as well as in the proportions of the structural elements (Fig. 3): in vascular plant cover (F = 6.500, p = .000), lichen cover (F = 80,173 p = .000), and bryophyte cover (F = 174,160, p = .000). The exposure of the plots did not, however, differ

Table 2. The number of plots in each of the 5 clusters (see Fig. 2) of sample plots on the grey dune ground layer vegetation with the cluster average total vegetation cover and average percentage cover of the vegetation elements: vascular plants, lichens and bryophytes. The range of variation of variables within the clusters is given in brackets. The average code values for plot exposure to compass directions are also shown (in "o'clock units", as on the face of watches).

Vegetation cluster	N of plots	Total cover % (range)	Vascular plant cover % (range)	Lichen cover % (range)	Bryophyte cover % (range)	Plot exposure (direction)
1	24	27 (14-51)	15 (5-25)	7 (0-20)	5 (0-20)	5.75 (SE-S)
2	10	82 (57-97)	8 (5-11)	51 (33-70)	24 (11-35)	5.05 (SE-S)
3	16	86 (61-99)	10 (3-25)	13 (1-26)	62 (43-80)	6.56 (S-SW)
4	11	85 (71-97)	7 (3-12)	34 (25-45)	44 (35-50)	6.82 (S-SW)
5	15	60 (43-85)	15 (5-30)	15 (6-25)	30 (20-40)	8.07 (SW-W)

Total vegetationcover	2	3	4	5
1	**.000**	**.000**	**.000**	**.000**
2	-	.934	.990	**.000**
3		-	.999	**.000**
4			-	**.000**
Vascularplantcover	2	3	4	5
1	**.008**	.071	**.002**	.999
2	-	.814	.998	**.033**
3		-	.592	.212
4			-	**.010**
Lichencover	2	3	4	5
1	**.000**	.052	**.000**	**.010**
2	**-**	**.000**	**.000**	**.000**
3		**-**	**.000**	.974
4			**-**	**.000**
Bryophytecover	2	3	4	5
1	**.000**	**.000**	**.000**	.152
2	**-**	**.000**	**.000**	**.000**
3		**-**	**.000**	**.000**
4			**-**	**.000**

Table 3. Results of the one-way ANOVA *post hoc* test (Tukey) on the localization of the differences between the vegetation clusters. Significant p –values are given in bold numbers.

between the clusters (F = 0.927, p = .453). The Tukey's *post hoc* test localize the significant differences in the variables between the clusters as follows: in total vegetation cover clusters 1 and 5 differ from each other and all the rest of the clusters (Table 3). In vascular plant cover the significant differences are scattered between the clusters 1 and 5 in comparison to the clusters 2 and 4, with no differences between the clusters 2, 3 and 4 (Table 3). Furthermore, the cluster 3 does not differ in vascular plant cover from any of the other clusters. In lichen cover almost all clusters differ from each other, except the cluster 3 from the clusters 1 and 5, and in bryophyte cover, all the other clusters except 2 and 5 differ significantly from each other (Table 3). The exposure did not differ significantly between any of the clusters in *post hoc* test.

The results of the Pearson correlation tests between the structural elements show significant negative correlation between total cover and vascular plant cover (Pearson Correlation -0.338, p = .003), but positive correlation to lichen and bryophyte cover (lichens: Pearson Correlation 0.666, p = .000, bryophytes: Pearson Correlation 0.840, p = .000). The correlation between vascular plant cover and the ground layer elements is negative (Lichens: -0.442, p = .000, Bryophytes: -0.386, p = .001). No significant correlation was detected between lichen and bryophyte cover. The total vegetation cover and the cover of the ground layer elements (lichens and bryophytes) show no significant correlation with the plot exposure. Vascular plant cover, however, shows significant correlation to exposure (Pearson Correlation 0.326, p = .004).

Discussion

The composition of the grey dune vegetation in the Curonian Spit Nature Reserve in Lithuania corresponds well to the previous studies by Stankevičiūtė (2000a, 2006). The sampled vegetation plots resample the description of the phytosociological class Koelerio-Corynephytorum. However, our material does not allow identification of more precise association, even though the general vegetation structure resamples the four associations described in Stankevičiūtė (2000a), especially as our samples contained only very little proportion of the vascular plants listed in previous studies.

The cluster analysis of our dataset on the grey dune vegetation reveals 5 clearly separable stages, which represent different conditions on the dunes. The cluster 1 has on average the lowest total cover (27 %) thus interpreted as a representive of the early successional stage. The average total cover is high in all the clusters 2 to 4, but they differ significantly in composition of the structural elements (Table 2, Fig. 3). The cluster 5 represents a stage characteristic to the ground layer vegetation of the Curonian spit grey dunes: after the ground layer cover reaches its maximum, the bryophyte and lichen species produce rounded plates which start to detach from each other (see the schematic illustration in Fig. 4). On the basis of our observations, bryophytes dominant in the early successional such as *Polytrichum piliferum* starts to get overgrown by the liverwort *Cephaloziella divaricata* as the bryophyte cover reaches its maximum represented by the clusters 2-4 (see also Fig. 4). Detachment of the ground layer plates create open spaces on the ground eventually giving free space to vascular plants, the average cover of which is slightly increasing again on the plots in the cluster 5 (Fig. 3). Furthermore, small scale disturbances caused by rain water currents and animal trampling on the fragile dune vegetation keep on the dynamic process of the vegetation development (see also discussion in Kalinauskaitė & Laaka-Lindberg, 2012).

The percentage cover of the structural elements vary between the clusters. The elements of the ground layer vegetation consisting of bryophytes and lichens reach soon high percentage cover in the middle stages 2-4. Our results do not, however, show correlation between the cover of these two vegetation elements. The colonization of bryophyte and lichen propagules is likely more or less random, and no facilitation of earlier colonizers is expected to those arriving later (see e.g. Jonsson & Esseen, 1990). The vascular plant cover is negatively correlated both to the total cover, and to other two structural elements. As the total cover increases, the cover of vascular plants goes down. However, as the ground layer elements start to form detached plates (Fig. 4), the flowering plant cover increases slightly (Fig. 3).

The proportions of structural elements forming the ground layer on grey dunes change along the succession (Fig. 3). We suggest that in the late stage, the ground layer species interactions start to play more important role, and open spaces are created for vascular plants to get established (Fig. 4).The vascular plants are more abundant on the plots in the early stages represented by cluster 1, but they are soon substituted by dense ground layer elements (clusters 2-4 in Fig. 3). In early stage vascular plants facilitate the establishment of bryophytes (see also Ingerpuu *et al.,* 2005), but eventually dense bryophyte cover starts to selectively effect vascular plants establishment, the grass species being less vulnerable than other flowering plants (Zamfir, 2000). The dominating growth-form (see *e.g.* Gimingham & Birse, 1957) of bryophyte species on grey dunes is short tufts, often with very high density. This enhances the water-holding capacity of the bryophyte-dominating ground layer. We suggest that in harsh environment of the dunes bryophyte water-holding capacity combined with the reducing sand movement by dense bryophyte tufts may facilitate the germination and establishment of *e.g.* tree seedlings. However, the effects of bryophytes on vascular plant germination and seedling establishment are not undisbuted (see *e.g.* Keizer *et al*., 1985; Zamfir, 2000; Michel *et al*., 2011).

On the basis of our observations, we propose that the role of bryophytes is central in the dynamics of the open grey dune vegetation with close interaction with terricolous lichens. The role of ground layer elements is essential for dune stabilizing and gradually the forest recovery in the strongly disturbed vegetation of the Curonian spit. Our further studies will be directed in more detail to the species interactions among the dominant elements of the grey dune ground layer vegetation.

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