



14<sup>th</sup> EURASIAN GRASSLAND CONFERENCE

# Semi-natural grasslands across borders

Post-conference excursion

9–11 July 2017, Western Lithuania

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2017-06-26. 60x90/16. Tiražas 50 egz.

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Spausdino UAB „Baltijos kopija“, Kareivių g. 13B, 09109 Vilnius

ISBN 978-9986-443-90-2

# Curonian Spit

## Introduction

The Curonian Spit has no analogues among other objects of the Baltic Region and Northern Europe because of its unique orographic parameters, geomorphological characteristics and geological composition as well as climatic peculiarity of the territory, mosaic of landscapes and concentration of numerous species of fauna and flora on its fairly small grounds.

The Curonian Spit is a 98 km long peninsula, extending in a long narrow strip from north to south. It separates the Curonian Lagoon from the Baltic Sea. Klaipėda strait is the northern boundary. Meanwhile, the southern part borders with the continent, the territory of Zelenogradsk city, Kaliningrad Oblast, Russia.

The widest place of the Spit (3.8 km) is the cape of Bulvikis Horn (*Bulvikio Ragas*), just four km northeast of Nida. Meanwhile, the narrowest place of 370 metres can be found in Lesnoy (Lithuanian: *Šarkuva*) settlement.

In Lithuanian part of the peninsula, five settlements are situated: Nida, Preila, Pervalka, Juodkrantė, Smiltynė, with approximately 4000 inhabitants. Curonian Spit National Park is visited by more than one million visitors every year. This is one of the most popular tourism destinations in Lithuania. That is why the biggest part of local inhabitants are working in tourism business.

Curonian Spit National Park was established in 1991. In 1961, the Cu-





Curonian Spit Landscape Reserve was founded, and in 1976, the peninsula was declared as National Forest Park. The Curonian Spit was included into the World Heritage List in 2000, as an outstanding example of landscape of sand dunes that is under constant threat of natural forces (wind and tide). After disastrous human interventions that menaced its survival, the Spit was reclaimed by massive protection and stabilization works in the 19th century and which are still continued to the present day (criterion v).

On the territory of the Republic of Lithuania, the biggest part of the Curonian Spit has been appointed as Natura 2000 territory. Coastal waters of the Baltic Sea are part of the HELCOM system of protected territories.

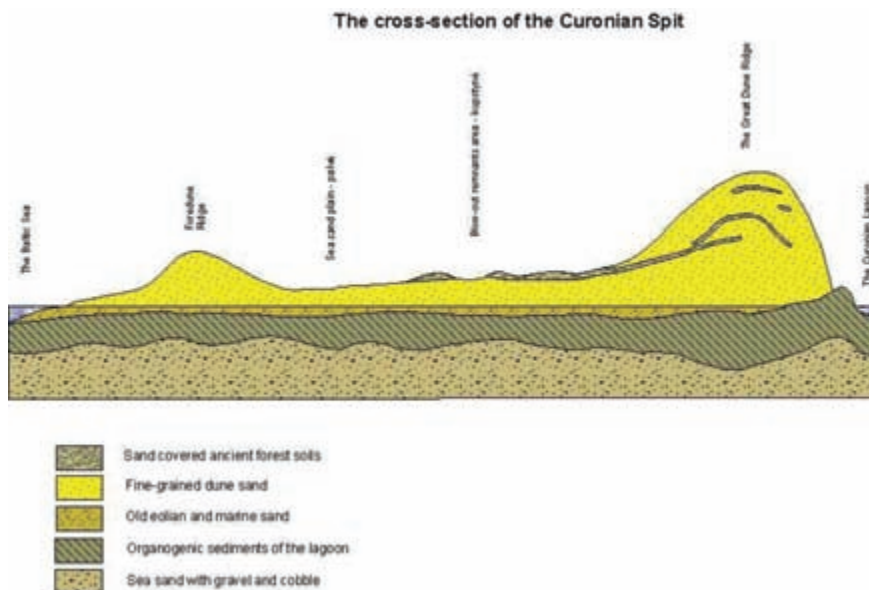
## Geology and geomorphology

Development of the present Curonian Spit started to the north of the Sambia (Lithuanian: Semba) Peninsula. Moving dunes covered the morainic ground and the swamp. Sand started to accumulate at Šarkuva and Rasytė islands, which were a natural barrier. Soon they joined the continent. Further growth of the spit went to the North and to the South. This process developed rather quickly and 4.500 or 4000 years ago the Curonian Spit reached the place, where Juodkrantė is presently located. Sand excess and prevailing west winds

formed the cross relief of the Curonian Spit. Sand hillocks at the seacoast were growing and the wind turned them into dunes, which were moving across the peninsula, making it wider. At the same time the peninsula moved eastward.

Nowadays, the Curonian Spit is the largest accumulative terrain formation in the Baltic region, formed by water and wind, with some of the highest sand-dunes in Europe. Over the centuries still moving sand-dunes and human activity trying to stop the dunes shaped especially vivid and attractive landscape complexes and objects, which creates the identity of the Curonian Spit: the Great Dune Ridge and its fragments (extend about 72 km, width from 250 m to 1.2 km, height 35–60 m), seaside horns and bays, the sea coast (beach and protective dune complex of the beach), the remaining virgin forests and newly planted mountain pines in the dunes.

Currently, natural processes of landscape formation in the Curonian Spit have still been going on, but are influenced by human activities. The relatively “young” age of the Curonian Spit determines its originality and high scientific value due to incomplete and still continuing process of formation.





## Climate

The climate of the Curonian Spit is a transitional one between marine and continental. Its specific feature is frequent and powerful changes in weather. One of the characteristic features of the climate is relatively mild winters and moderately warm summers: the annual temperature averages  $7.0^{\circ}\text{C}$ , the absolute minimum being  $-26^{\circ}\text{C}$  (January) and the absolute maximum amounting to  $31^{\circ}\text{C}$  (June). The average precipitation is 660 mm, most of which falls in October and February. The formation of the snow blanket is highly varied: sometimes the snow blanket is non-existent, while at other times it reaches 30–60 cm.

The Curonian Spit has up to 40 stormy days per year on average when the wind force exceeds 15 m/s, leaving negative effects on the shores, forests and settlements. The Curonian Spit was devastated by an extremely strong storm of 1993, the hurricane Anatol in 1999 and the hurricane Erwin in 2005. Strong storms have become more frequent due to a more intensive cyclone action as a result of climate change, and periods of calm weather have grown shorter.

## Landscape history

The history of Curonian Spit is dramatic: 5.000 years ago a narrow peninsular, the Great Dune Ridge, separating the Baltic Sea from the Curonian Lagoon, was formed on moraine islands from the sand transported by currents and later covered by forest. Deforestation, intensive animal grazing, resin mining, tapping and bushfires were going on since the 16th century. Deforestation was lasting for almost 200 years. The percentage of the forest covered area in the Curonian Spit decreased from 75% (1605) to 10% (1834). The dunes began moving towards the Curonian Lagoon burying the oldest settlements, so that at the turn of the 18th to the 19th century it became evident that human habitation was no longer possible here if no deliberate action was taken. At that time the dune stabilization works began, which have been continued for 200 years till today. By the end of the 19th century, a protective dune ridge was formed along the seashore, which prevented sand migration inland and the Great Dune Ridge was reinforced using brushwood hedge and by planting trees – mostly mountain pine (*Pinus mugo*). The first samplings of this pine were transported from Denmark, later – grown in the Spit.



Formation of the coastal foredune ridge (beginning of the 20th century)

Currently, forests and sands dominate in the Curonian Spit. Forests make up 74% of the total territory; urbanised areas (eight small settlements) cover just about 3%.



## Culture

The human history of the Curonian Spit is closely related to the fishing and fishermen. Poor soil restricted the ability of local people engaged in livestock and crop production, that is why the fishing and all attributes of that formed tangible and intangible culture of the Curonian Spit and till now can be observed in all settlements. The 19th–20th century was the period of a fishing villages' transition into a resort. At first, the changes came to Juodkrantė, later – to Nida. This period brought trendy fashion, entertainment, and above all a new architectural style and resort infrastructure in the Curonian Spit. The Curonian Spit as a unique place was discovered by prof. Adalbert Bezzenberger, neurologist Sigmund Freud, geographer Alexander Von Humboldt, writer Thomas Mann, novelist Jean-Paul Sartre, painters Lovis Corinth, Max Pechstein and many others.

Ethnic composition of the inhabitants of the Curonian Spit varied from the old times. The records of the 14th–16th centuries mention the Curonians and Germans residing there. Lithuanians (so called *Lietuvinkaĩ*) were also men-



tioned along with them in the 16th–20th centuries. In the 19th –20th centuries, a kind of trilingual culture appeared in the Curonian Spit: German was used for daily communication at state authorities, Curonian – while fishing, Lithuanian – in church services. The Second World War essentially changed ethnic composition of the Curonian Spit residents. Majority did not return back after the autumn evacuation in 1944, a significant amount of population moved to Germany in 1958, and their place was filled by newcomers from the other regions of Lithuania or even from the Soviet Union.



The Kurenkahn (*Kurėnas*) – a traditional flat-bottomed boat



Gravestone monuments – *krikštai* – at Nida ethnographic cemetery

## Biodiversity

A distinguishing feature of the Curonian Spit is an extraordinary diversity of nature and communities contrasts that exist side by side: the beaches, marshes, brackish and freshwater bodies, meadows, pine forests, deciduous forests (alder, birch) and sand dunes. This creates a specific diversity of animals and plants in a relatively small and limited area.

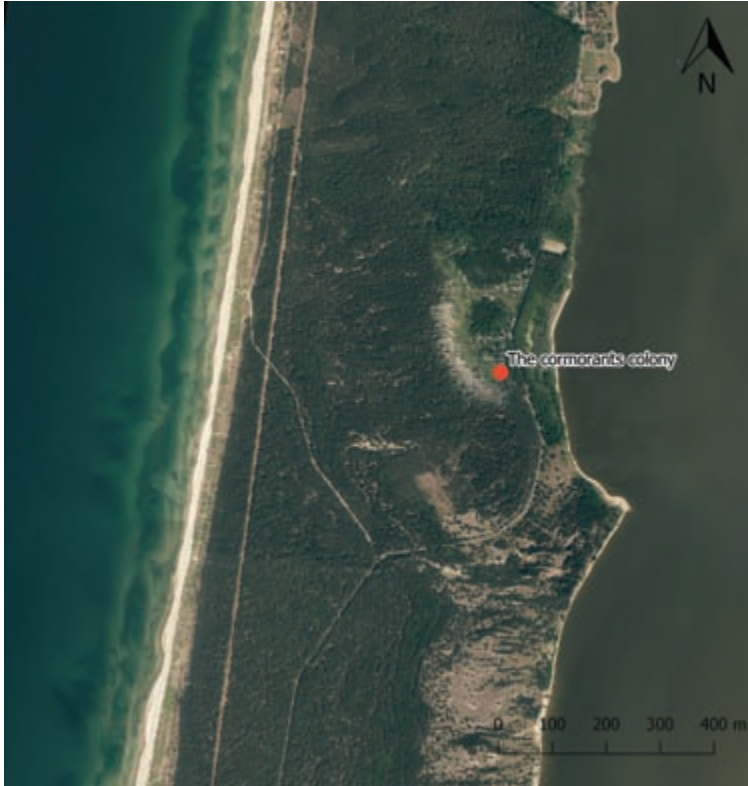
In the Curonian Spit, eight habitats of European importance are identified: 2110 Embryonic shifting dunes, 2120 Shifting dunes along the shoreline with *Ammophila arenaria* („white dunes“), 2130 \* Fixed coastal dunes with herbaceous vegetation („grey dunes“), 2140 \* Decalcified fixed dunes with *Empetrum nigrum*, 2170 Dunes with *Salix repens* ssp. *argentea* (*Salicion arenariae*), 2180 Wooded dunes of the Atlantic, Continental and Boreal region, 2190 Humid dune slacks, 2320 Dry sand heaths with *Calluna* and *Empetrum nigrum*. Curonian Spit is the area of European importance for breeding White-tailed sea-eagle (*Haliaeetus albicilla*), Woodlarks (*Lullula arborea*), Tawny pipit (*Anthus campestris*). Curonian Lagoon and the Baltic Sea waters at the coast of the Curonian Spit are important place for migratory Little gulls (*Larus minutus*) and Common terns (*Sterna hirundo*), wintering Velvet scoters (*Melanitta fusca*) and razorbills (*Alca torda*).



*Salsola kali*

## Excursion sites

### Great cormorant colony



**The Grey heron and Great cormorant colony** by Juodkrantė is one of the biggest colonies of grey herons and grand cormorants in Lithuania. People have been observing this colony since the end of the 19th century. Currently, there are more than 2900 grand cormorant nests and about 270 grey heron nests. The first cormorants in the Curonian Spit appear in early February and soon after grey herons follow them as well. The colony revives in late March. The birds share out and put in order their old nests, build new ones. Soon pairs start sitting. In May, every nest has from three to five young birds. In autumn, everything calms down and the colony stays silent till the next season.



Due to a rapid growth of the population and degradation of old forest since 2007 the growth of colony has been regulated. The regulation measures are implemented in the spring time during hatching period through cooling off the eggs.



## Nagliiai



**The Nagliai Strict Nature Reserve** covers an area of 1669 ha, where coastal grassland from *Ammophiletea* and *Koelerio-Corynepherea* of white and grey dunes dominate.

See detailed vegetation characteristic in the material presented below (Stankevičiūtė, 2006).

This Reserve is a sanctuary for a number of species, which are included in the Red List: plants – Baltic toadflax (*Linaria loeselii*) – endemic species of the southeastern coast of the Baltic Sea, species of the Habitats Directive (Annex 2), – Seaside centaury (*Centaurium litorale*), Sea-holly (*Eryngium maritimum*), Lesser twayblade (*Listera cordata*), Shining crane's-bill (*Geranium lucidum*); fungus – *Pycnoporus cinnabarinus* and *Peziza ammophila*; insects – Striped earwig (*Labidura riparia*), Pine chafer (*Polyphylla fullo*) and Coastal tiger-beetle (*Cicindela maritima*); birds – Tawny pipit (*Anthus camp-*

*estris*), Ringed plover (*Charadrius hiaticula*) and Common shelduck (*Tadorna tadorna*). The White-tailed sea-eagle (*Haliaeetus albicilla*) is frequent visitor there, too.

Any human activity, including recreation, is prohibited in the Reserve. Nature is preserved for scientific purposes to study natural processes in dune ecosystems.





*Linaria loeselii*



*Tragopogon heterospermus*

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## THE SUCCESSION OF SAND VEGETATION AT THE LITHUANIAN SEACOAST

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## Abstract

Stankevičiūtė J., 2006: The succession of sand vegetation of Lithuanian seacoast [Lietuvos pajūrio smėlynų augalijos sukcesija]. – *Botanica Lithuanica*, 12(3): 139–156.

The paper aims to define the autogenic succession of sand vegetation of the Baltic Sea coast of Lithuania. The succession sequence of plant communities situated in Lithuanian seacoast, located in the direction from West to East, was created. The regularities of sand communities succession were revealed. Only species (*Ammophila arenaria*, *Honckenya peploides*, *Leymus arenarius*, *Calamagrostis epigejos*) adapted to the growth on dry sand form short-lived thickets on the seashore. The communities situated in different places of foredunes perform different functions: species-poor *Leymo-Ammophiletum* subas. *typicum* and *Leymo-Ammophiletum* subas. *petasitetosum* communities located on the western slope consist of psammophytes that fasten the drifting sand; the two layer grassland of *Leymo-Ammophiletum* subas. *festucetosum sabulosae* located on the top of the foredunes decreases the fluctuations of temperature and humidity; in the two-layer (herb and moss layers) *Leymo-Ammophiletum* subas. *artemisietosum* stretching on the eastern slope humus begins to accumulate. In palve the drifted sand is stopped by the abundantly growing *Carex arenaria*, *Corynephorus canescens*, *Festuca sabulosa*, *Festuca polesica*, solitary, thick groves of *Empetrum nigrum*, and the continuous cover of moss and lichens. In palve strength of winds and irreciprocal stream is reduced and dispersed by abundantly growing shrubs of *Salix rosmarinifolia*, *Salix daphnoides*, and low *Pinus sylvestris* and *Betula pendula* trees. In the primary forest communities *Pinus sylvestris* is abundant in tree layer. In further succession stages *Pinus sylvestris* gets thinner. In herb layer the dominant plants with wide ecologic range are replaced by plants characteristic for forest communities (*Deschampsia flexuosa*, *Melampyrum nemorosum*, *Luzula multiflora*, *Trientalis europea*, *Majanthemum bifolium*), bryophytes get thicker, leaf-litter forms, the amount of humus increases. It was revealed that the edaphic climax of sand vegetation in Lithuanian seacoast corresponds to *Leymo-Ammophiletum arenariae*, while climatic climax – to *Quercus-Piceetum* communities.

**Keywords:** succession, endoecogenesis, syngeneses, vegetation, foredune, palve, Curonian Spit, Baltic Sea coast, Lithuania.

## INTRODUCTION

Lithuanian seacoast is a dynamic zone where different components comprise a natural environment. Eventually, high diversity of ecotopes and plant commu-

nities forms under the affects of the sea and the edaphic gradient influences the succession sequence.

Sand dune systems offer an ideal opportunity to study vegetation succession. Vegetation succession is one of the fundamental ecological concepts that underpin

our understanding of the habitat development and their management (OLFF et al., 1993). The obvious sign of succession is a change in the plant community, but the process of soil development, occurring during the succession, is also of great importance (BAKKER & DIGGELEN, 2006). The sand dune transects offer an opportunity to observe the parallel processes of vegetation succession and soil development. Dune systems are particularly suitable for observation of community succession, as the new dunes are being formed by geomorphological processes on the seaward side, while on the landward side dunes that have formed centuries before are stabilized and colonized by plants, thus representing the process of community succession (OLFF et al., 1993). The geomorphological and ecological processes are not operating independently, but are closely related and dependant upon one another.

Changes of seacoast sand vegetation in different regions of the Baltic Sea are widely investigated (PIOTROWSKA, 1965; FISCHER, 1998; WOJTAŃSKI, 1993; DOLNIK, 2003). However, due to peculiarities of the Lithuanian coast, it is impossible to accept directly the peculiarities of vegetation change observed in other regions; therefore, the investigations of vegetation changes in Lithuanian seacoast are relevant theoretically and practically.

Since December 2000 the Kuršių Nerija National Park has been included into UNESCO World Heritage List as valuable cultural landscape. Large area of continental part of the Lithuanian seacoast belongs to the Pajūris Regional Park. It is a governmentally protected territory of the Lithuanian seaside from Klaipėda to Palanga. Pajūris Regional Park was established on September 24, 1992 in order to protect beautiful landscapes of the seaside, natural and cultural values, biological diversity of the Baltic Sea, re-establish destroyed or broken natural and cultural values, and at the same time provide conditions for cognitive tourism and lounge development.

## MATERIAL AND METHODS

The investigations were carried out on the Lithuanian seacoast during 1995–2001. Phytocenotic and floristic material was collected in the Curonian spit and on the seacoast from Klaipėda to Šventoji (Fig. 1). In the Curonian Spit the geobotanical relevés were described in the entire cross-section from the sea to the lagoon, at the interval of 1 km from each other, leaving out the settlements and zones of recreation. In the continental part of the seacoast, the transect lines were also directed from the West towards the East, starting at the beach and ending anywhere by anthropogenised ecotops. The de-



Fig. 1. Areas of investigation at Lithuanian seacoast

scribed communities are situated on different geomorphological forms, naturally occurring in the coastal area.

Ecological parameters of ecotopes were investigated. Soil type, pH, amount of humus and nutrients were evaluated. Soil analysis was performed at the Laboratory of Chemical Analysis of the Institute of Botany. The following agrochemical properties of soil were analysed:  $\text{pH}_{\text{KCl}}$  – by potentiometry,  $\text{P}_2\text{O}_5$  – by photoelectrocolorimetry (using ammonium molybdate),  $\text{K}_2\text{O}$  – by flame photometry,  $\text{N}_{\text{total}}$  – by photoelectrocolorimetry (using sulphur acid and hydrogen peroxide),  $\text{CaCO}_3$  –



by titration, humus – by photoelectrocolorimetry (oxidizing with potassium dichromate in acid medium).

The differentiation of geomorphological structures of the Lithuanian seacoast by GUDELIS (1998) and characterization of aeolian processes in seacoast by ŽILINSKAS (2001) were used in this work.

As one of parameters, Koch index of biological dispersion ( $K_k$ ) (STANKEVIČIŪTĖ, 1995), also known as Koch coefficient (MIRKIN & ROZENBERG 1983), was used for ascertaining the dynamics, succession and transitional stages of plant communities.

$$K_k = \frac{T-S}{(n-1) \cdot S}$$

$S$  – number of species in a community;

$$T = \sum_{i=1}^n S_i$$

$n$  – number of relevés in a table.

The value obtained was multiplied by 100 %. The communities with  $K_k$  higher than 30 % were chosen as succession stages, and those with  $K_k$  value lower than 30 % – transitional stages.

Phytocenotic relevés were made according to the principles of BRAUN-BLANQUET (1964). Relevé area of sand communities was 10 × 10 m, of forest communities – 10 × 20 m.

While describing forest communities, three levels were distinguished in the tree layer:

A 1 – trees higher than 6 m;

A 2 – trees up to 6 m height;

A 3 – undergrowth, the layer of trees and bushes of about 1 m height.

Small shrubs were attributed to the herb layer. Moss and lichen layers were evaluated separately.

Syntaxonomical position of communities was ascertained using the classification schemes of BANDŽILIENĖ (1977), KORNECK (1978), MATUSZKIEWICZ (1984; 1996; 2001), POTT (1992), DIERSSEN (1996), STANKEVIČIŪTĖ (2000).

Names of taxa of vascular plants, mosses and lichens are used according to GREUTER (1993), JANKEVIČIENĖ (1998), GUDŽINSKAS (1999), MOTIEJŪNAITE (1999), JUKONIENĖ (2003).

## AUTHOGENIC SUCCESSION OF SAND VEGETATION IN LITHUANIAN SEACOAST

Plant communities are influenced by many biotic and edaphic factors, though the combination and balance of these factors influence the structure of communities. Autogenic succession is divided into endocogenesis and syngeneses according to the character of factors sti-

mulating and limiting change of plant communities (MIRKIN & ROZENBERG, 1978). The sea vicinity and related climatic and orographic conditions influence coastal vegetation (POTROWSKA, 1965; OLIF ET AL., 1993; BAKKER & DIGGILEN, 2006).

## SUCCESSION OF THE SAND VEGETATION ON THE FOREDUNE

In Lithuanian seacoast, the beach is an initial point of the sequence of plant communities change. Here the diversity of species composing plant communities totally depends on such edaphic factors as wind, shifting sand, wave impact, fluctuations of temperature and humidity. The vegetation succession starts with the process of endocogenesis. Plants adapted to the growth on dry sand, e.g. *Honckenia peploides*, *Cakile maritima*, rarely *Ammophila arenaria*, *Calamagrostis epigejos*, form short-lived (surviving only one vegetation period) monodominant thickets. A lot of limiting edaphic factors and short-lived thickets formed by 4–5 plant species are the conditions at the initial point of autogenic succession.

Next ecological zone, moving landward, is a foredune (Fig. 2). Here relief forms change, and the number of plant species and the projection coverage increase, vegetation layers start differentiating. On the western slope of foredunes shifting sand dominates (ŽILINSKAS, 2001). Therefore, the communities of the *Leymo-Ammophiletum* subas. *typicum* and *Leymo-Ammophiletum* subas. *petasitetosum* are situated on the western slope of foredunes. They consist of a few species and hold up the shifting sand. The edificators of these communities are tall grasses *Ammophila arenaria*, *Calamagrostis epigejos*, *Leymus arenarius*, which are adapted to grow in permanently shifting powdery sand, poor in nutrients. The sand moving landward through the beach accumulates near tussocks, and thick aboveground parts of plants dissipate sand flow. *Petasites spurius* and *Honckenia peploides*, growing abundantly in these communities and making thick tussocks among tall grasses, are important for stabilization of shifting sand. The lack of humidity on the top of foredunes is the main community-limiting factor (ŽILINSKAS, 2001). *Ammophila arenaria*, *Leymus arenarius*, *Festuca arenaria* do not form tussocks. These plants grow abundantly and form a dense tall herb layer. In the low herb layer *Festuca sabulosa*, *Tragopogon heterospermus*, *Linaria loeselii* grow abundantly. The grassland of two levels of the *Leymo-Ammophiletum* subas. *festucetosum sabulosae* communities, situated on the top of foredunes, reduces the fluctuations of temperature and humidity.



Fig. 2. Distribution of the sand vegetation in cross-section, in the Curonian Spit near Juodkrantė (55/56; 57 forest blocks). 1 – single *Cakile maritima*, *Salsola kalii*, *Honckenya peploides* tussocks; 2 – *Leymo-Ammophiletum* subas. *typicum* and *Leymo-Ammophiletum* subas. *petasitetosum*; 3 – *Leymo-Ammophiletum* subas. *festucetosum sabulosae*; 4 – *Leymo-Ammophiletum* subas. *artemisiyetosum*; 5 – *Carex arenaria* stage communities; 6 – *Helichryso-Jasionetum*; 7 – *Empetrum nigrum* stage communities; 8 – *Betula pendula* stage communities; 9 – *Alnus glutinosa* stage communities; 10 – *Empetrum nigri-Pinetum* subas. *typicum*; 11 – *Empetro nigri-Pinetum* subas. *cladonietosum*; 12 – *Empetro nigri-Pinetum* subas. *pyroletosum*; 13 – *Pinus mugo* thickets; 14 – *Violo-Corynephorretum canescens*

On the eastern slope of foredunes edaphic conditions are different. Because of lee, sand is less subjected to shifting. Humidity changes gradually due to gently sloping and high groundwater level (ŽILINSKAS, 2001). Here are two layers (herb and bryophyte) of the *Leymo-Ammophiletum* subas. *artemisiyetosum* communities. *Artemisia campestris*, *Lathyrus maritimus*, *Gypsophila paniculata*, *Thymus serpyllum*, *Tragopogon heterospermus*, *Carex arenaria*, *Galium verum*, *Ammophila arenaria*, *Calamagrostis epigejos* dominate in the herb layer. Dense moss layer consists of *Ceratodon purpureus*, *Racomitrium canescens*, *Polytrichum piliferum*, *Brachythecium albicans*. In communities situated on the eastern slope of the foredune, humus starts to accumulate. Nevertheless, the structure and diversity of species in the communities occurring in separate parts of the foredunes change, and the group of plants, dominating and forming communities in the first stage of shifting sand overgrowth, remains unchanged (Table 1). It consists of *Ammophila arenaria*, *Leymus arenarius*, *Festuca arenaria*, *Honckenya peploides*, *Lathyrus maritimus*, *Tragopogon heterospermus*.

#### CHANGES OF PLANT COMMUNITIES OF PALVE

In the ecological zone of palve (Fig. 2) the inversion of the impact of edaphic factors on vegetation is evident. They do not limit but sustain the stimulating role of the change of vegetation. High (0.7–1 m) groundwater level

(GUDELIS, 1998), lee (the foredunes up to 12 m high), even distribution of outwashed nutrients and precipitation amount (ŽILINSKAS, 2001) form a combination of edaphic factors highly favourable for the vegetation. According to the relief and humidity conditions, palve is divided into the grassland palve, flooded palve, and hillocky palve (GUDELIS, 1998). The plant communities located in palve are different according to their age and structure (Table 2).

**Grassland palve** starts just after the foredunes. Deflation focuses form in small areas, because of mechanical damage of the foredunes, sand slump, unearthing of wild boars, intensive recreation and economic activities. Dominating whirling winds do not transfer large amount of sand but continuously move surface sand layer (ŽILINSKAS, 2001). The main role in the stabilisation of sand movement and stopping further deflation processes fall to the *Carex arenaria* communities. The edifier of these communities *Carex arenaria* as well as *Ammophila arenaria* have long rhizomes and easily develop new vegetative shoots. As weak whirling wafts prevail, *Carex arenaria* does not form thick overgrowths. Most frequently *Carex arenaria* vegetative plants grow distantly from each other forming concentric overlapping circles thus making a possibility for other plant species to settle between them. *Carex arenaria*, *Festuca sabulosa*, *Jasione montana* make a group of ecotonic species, associating communities of the foredunes and palve. In palve the *Carex arenaria* commu-



Table 1.

The dominating communities in the first moving sand overgrowth stage in the foredunes ecological zone. Syn 1 – *Leymo-Ammophiletum* subas. *typicum*; 2 – *Leymo-Ammophiletum* subas. *patasitetosum*; 3 – *Leymo-Ammophiletum* subas. *festucetosum sabulosae*; 4 – *Leymo-Ammophiletum* subas. *artemisietosum*

Syntaxa	1	2	3	4
Number of relevés	17	15	15	10
Total number of species	12	22	29	35
Average number of species	6	11	13	16
Coverage (%)				
tree layer	.	.	.	.
shrub layer	.	.	.	.
herb layer	52	47	77	52
bryophyte layer	.	.	8	34
lichen layer	.	.	.	.
1	2	3	4	5
<i>Calamagrostis epigejos</i>	V <sup>1-3</sup>	V <sup>+2</sup>	III <sup>1-2</sup>	IV <sup>+2</sup>
<i>Hieracium umbellatum</i>	IV <sup>+</sup>	IV <sup>+</sup>	V <sup>+1</sup>	V <sup>+2</sup>
<i>Gypsophila paniculata</i>	II <sup>+</sup>	IV <sup>+2</sup>	V <sup>+2</sup>	V <sup>+3</sup>
<i>Ammophila arenaria</i>	V <sup>1-3</sup>	V <sup>1-2</sup>	V <sup>+3</sup>	IV <sup>+3</sup>
<i>Leymus arenarius</i>	V <sup>+3</sup>	V <sup>+2</sup>	IV <sup>+2</sup>	IV <sup>+2</sup>
<i>Lathyrus maritimus</i>	V <sup>+1</sup>	V <sup>+2</sup>	V <sup>+1</sup>	V <sup>+2</sup>
<i>Honckenya peploides</i>	IV <sup>+</sup>	V <sup>+</sup>	V <sup>+1</sup>	IV <sup>+</sup>
<i>Festuca arenaria</i>	IV <sup>+2</sup>	V <sup>+2</sup>	III <sup>+2</sup>	III <sup>+2</sup>
<i>Tragopogon heterospermus</i>	II <sup>+</sup>	III <sup>+</sup>	III <sup>+</sup>	IV <sup>+</sup>
<i>Linaria loeselii</i>	II <sup>+</sup>	IV <sup>+</sup>	I <sup>+</sup>	.
<i>Salix daphnoides</i>	I <sup>+</sup>	II <sup>+</sup>	I <sup>1-2</sup>	I <sup>2</sup>
<i>Rosa rugosa</i>	II <sup>+</sup>	.	II <sup>+2</sup>	I <sup>1</sup>
<i>Petasites spurius</i>	.	V <sup>+2</sup>	.	.
× <i>Calammophila baltica</i>	.	III <sup>+2</sup>	.	.
<i>Salsola kali</i>	.	III <sup>+</sup>	.	.
<i>Oenothera biennis</i>	.	III <sup>+</sup>	.	.
<i>Cakile baltica</i>	.	II <sup>+</sup>	.	.
<i>Carex arenaria</i>	.	II <sup>1</sup>	III <sup>+1</sup>	V <sup>+2</sup>
<i>Festuca sabulosa</i>	.	II <sup>+2</sup>	V <sup>1-3</sup>	IV <sup>1-3</sup>
<i>Jasione montana</i>	.	.	IV <sup>+1</sup>	II <sup>+1</sup>
<i>Galium verum</i>	.	I <sup>+</sup>	I <sup>+</sup>	III <sup>1-2</sup>
<i>Brachythecium albicans</i>	.	I <sup>+</sup>	II <sup>1-2</sup>	II <sup>+2</sup>
<i>Polytrichum piliferum</i>	.	I <sup>+</sup>	I <sup>+</sup>	III <sup>1-3</sup>
<i>Ceratodon purpureus</i>	.	.	I <sup>+2</sup>	III <sup>+2</sup>
<i>Corynephorus canescens</i>	.	.	II <sup>+1</sup>	II <sup>+</sup>
<i>Rumex acetosella</i>	.	.	I <sup>+</sup>	I <sup>+</sup>
<i>Viola littoralis</i>	.	.	I <sup>+</sup>	I <sup>+</sup>
<i>Sedum acre</i>	.	.	I <sup>+</sup>	II <sup>+</sup>
<i>Cetraria aculeata</i>	.	.	I <sup>+</sup>	II <sup>+2</sup>
<i>Galium album</i>	.	.	II <sup>+</sup>	II <sup>+</sup>
<i>Cladonia miris</i>	.	.	I <sup>+</sup>	I <sup>+</sup>
<i>Artemisia campestris</i>	.	II <sup>+</sup>	.	V <sup>+1</sup>
<i>Viola tricolor</i>	.	.	.	III <sup>+</sup>
<i>Racomitrium canescens</i>	.	.	.	III <sup>+2</sup>
<i>Astragalus arenarius</i>	.	.	.	III <sup>+1</sup>

Table 1 (continued).

1	2	3	4	5
<i>Anthyllis vulneraria</i>	-	+	-	III <sup>++2</sup>
<i>Epipactis atrorubens</i>	-	+	-	II <sup>+</sup>
<i>Eryngium maritimum</i>	-	-	I <sup>+</sup>	I <sup>+</sup>
<i>Pohlia nutans</i>	-	-	I <sup>+</sup>	I <sup>+</sup>
<i>Dicranum scoparium</i>	-	-	I <sup>+</sup>	-
<i>Pseudoscleropodium purum</i>	-	-	-	II <sup>+</sup>
<i>Conyza canadensis</i>	-	-	-	I <sup>+</sup>

nities neighbour upon the *Helichryso-Jasionetum* communities, which occupy the largest part of grassland palve. Plant communities of palve are considered as the second stage of the succession of sand vegetation. The group of plants, dominating and forming communities at this stage, consists of *Helichrysum arenarium*, *Cardaminopsis arenosa*, *Thymus serpyllum*, *Koeleria glauca*, *Empetrum nigrum*, *Salix rosmarinifolia*, *Pinus sylvestris* A3. In *Carex arenaria* stage communities, the species characteristic to white dunes strongly decrease or disappear. The *Helichryso-Jasionetum* communities are characteristic only to palve and correspond to the optimal climatic conditions. They distinguish by a high number of mosses and lichens (*Brachythecium albicans*, *Ceratodon purpureus*, *Polytrichum gracile*, *Racomitrium canescens*, *Cladonia mitis*, *Cladonia cornuta*, *Cladonia rangiferina*, *Cetraria aculeata*, *Peltigera canina*). Initial forest communities start to form, single small (up to 0.5 m height) *Pinus sylvestris* trees and *Salix rosmarinifolia* shrubs start to grow in herb layer.

**Plane flooded palve** occurs only in the southern part of the Spit, in the area between Preila and Nida. This part of palve is flooded by water for a long period or even permanently during more humid years.

This ecological zone is characterised by various succession stages of the *Alnus glutinosa* communities where tree layer is formed by *Alnus glutinosa*, *Betula pendula*, and occasional, non-typical *Pinus sylvestris*. *Dryopteris carthusiana*, *Moehringia trinervia*, *Urtica dioica*, *Stellaria media*, *Rubus idaeus*, *Deschampsia flexuosa*, *Scutellaria galericulata*, *Galium boreale*, *Mycelis muralis*, *Trientalis europaea* comprise the herb layer. The occurrence of other herbs in the community depends upon the water level. *Melampyrum nemorosum*, *Anthoxanthum odoratum*, *Rumex acetosella*, *Geranium robertianum*, *Maianthemum bifolium* prefer drier ecotopes, while *Calamagrostis canescens*, *Lysimachia thyrsiflora*, *Impatiens noli-tangere* occur in wetter sites. The variety of herb layer species changes due to water accumulation at the soil surface. The change of *Alnus glutinosa* communities structure should be more precisely

called seasonal fluctuations but not succession. Mosses are almost absent in these communities.

Sand communities prevail on the seacoast, thus *Alnus glutinosa* communities, reliant on the excess of humus and humidity, are the reflexion of local changes in edaphic conditions.

**Hillocky palve** (eastern part of the grassland palve). *Empetrum nigrum* and *Betula pendula* communities stretch in this ecological zone.

The *Empetrum nigrum* communities are the last stage of herb communities changing to forest. These communities cover a narrow zone of 10–20 m just beside the grassland palve and occur on accumulative hummocks of sand. *Empetrum nigrum* forms dense overgrowths of 4 × 4 m or 5 × 5 m in these communities. *Salix rosmarinifolia* grows abundantly here as well as small, up to 1 m height, *Pinus sylvestris* and *Betula pendula* trees. These communities occupy an ecotonic area regarding the structures of the variety of plants and relief. Certain plants, characteristic to herb layer of palve, dominate here (*Carex arenaria*, *Jasione montana*, *Corynephorus canescens*, *Viola tricolor*, *Fragaria vesca*), and plants of neighbouring forest communities (*Deschampsia flexuosa*, *Melampyrum nemorosum*, *Trientalis europaea*) appear. The cover of mosses is dense due to *Pleurozium schreberi*, *Pseudoscleropodium purum*, *Dicranum polysetum*, characteristic of forest communities, and *Brachythecium albicans*, *Ceratodon purpureus*, *Polytrichum piliferum*, characteristic of sand communities.

Comparison of species combinations forming the communities of seacoast foredunes and palve as well as their functions reveals the continuity of plant ecological significance:

1. Instead of *Ammophila arenaria*, *Calamagrostis epigejos*, *Leymus arenarius*, *Festuca arenaria* growing on the seacoast foredunes, in palve the main holders of sand are *Carex arenaria*, *Corynephorus canescens*, *Festuca sabulosa*, *Festuca polesica*.

2. The two-level herb layer consisting of *Ammophila arenaria*, *Calamagrostis epigejos*, *Carex arenaria*, *Festuca sabulosa*, *Honckenya peploides*, which insures

Table 2.

The dominating communities in the second overgrowth stage in the ecological zone of palve. Syntaxa: 1 – *Carex arenaria* communities; 2 – *Violo-Corynephorum canescentis*; 3 – *Helichryso-Jasionetum*; 4 – *Empetrum nigrum* communities

Syntaxa	1	2	3	4
Number of relevés	10	37	33	15
Total number of species	43	58	82	89
Average number of species	24	14	28	17
Coverage (%)				
tree layer	-	-	6	21
shrub layer	-	-	5	10
herb layer	62	60	55	48
bryophyte layer	12	20	28	33
lichen layer	16	40	23	28
1	2	3	4	5
<i>Calamagrostis epigejos</i>	IV <sup>+1</sup>	III <sup>+</sup>	IV <sup>+</sup>	II <sup>+</sup>
<i>Hieracium umbellatum</i>	V <sup>+2</sup>	V <sup>+2</sup>	V <sup>+</sup>	IV <sup>+</sup>
<i>Gypsophila paniculata</i>	II <sup>+2</sup>	I	IV <sup>+2</sup>	II <sup>+1</sup>
<i>Carex arenaria</i>	V <sup>2-3</sup>	V <sup>+3</sup>	V <sup>1-2</sup>	V <sup>1-3</sup>
<i>Festuca sabulosa</i>	V <sup>+4</sup>	IV <sup>+2</sup>	IV <sup>1-2</sup>	III <sup>+2</sup>
<i>Jasione montana</i>	V <sup>+2</sup>	V <sup>+3</sup>	IV <sup>+3</sup>	V <sup>+2</sup>
<i>Ammophila arenaria</i>	III <sup>+2</sup>	II <sup>+2</sup>	-	-
<i>Leymus arenarius</i>	-	I <sup>+</sup>	II <sup>+</sup>	-
<i>Lathyrus maritimus</i>	IV <sup>+2</sup>	I <sup>+</sup>	II <sup>+</sup>	-
<i>Honckenya peplodes</i>	II <sup>+</sup>	-	II <sup>+</sup>	-
<i>Festuca arenaria</i>	II <sup>+</sup>	I <sup>+</sup>	II <sup>+</sup>	-
<i>Tragopogon heterospermus</i>	III <sup>+</sup>	I	I <sup>+</sup>	-
<i>Linaria loeselii</i>	I	I	I <sup>+</sup>	I
<i>Salix daphnoides</i>	I	I	I <sup>1</sup>	-
<i>Galium verum</i>	I	I	III <sup>1</sup>	I
<i>Brachythecium albicans</i>	II <sup>1</sup>	II <sup>+2</sup>	III <sup>+1</sup>	II <sup>+1</sup>
<i>Polytrichum piliferum</i>	I	V <sup>+4</sup>	III <sup>+2</sup>	II <sup>+2</sup>
<i>Ceratodon purpureus</i>	-	III <sup>+2</sup>	III <sup>+2</sup>	II <sup>+</sup>
<i>Corynephorus canescens</i>	II <sup>1-2</sup>	V <sup>1-3</sup>	III <sup>1-3</sup>	II <sup>1</sup>
<i>Cladonia mitis</i>	II <sup>1-2</sup>	V <sup>+4</sup>	III <sup>1-4</sup>	III <sup>+4</sup>
<i>Racomitrium canescens</i>	-	III <sup>1-2</sup>	II <sup>+2</sup>	-
<i>Helichrysum arenarium</i>	II <sup>2</sup>	II <sup>+1</sup>	IV <sup>+</sup>	III <sup>+1</sup>
<i>Cardaminopsis arenosa</i>	II <sup>+</sup>	II <sup>+</sup>	III <sup>+</sup>	II <sup>+</sup>
<i>Thymus serpyllum</i>	I	II <sup>1</sup>	V <sup>+</sup>	II <sup>+</sup>
<i>Festuca polesica</i>	II <sup>1-3</sup>	IV <sup>+2</sup>	III <sup>+1</sup>	I
<i>Koeleria glauca</i>	-	-	IV <sup>+2</sup>	I
<i>Pilosella officinarum</i>	-	III <sup>+</sup>	II <sup>+2</sup>	II <sup>+</sup>
<i>Rumex acetosella</i>	II <sup>2</sup>	II <sup>+</sup>	III <sup>+</sup>	II <sup>+</sup>
<i>Viola litoralis</i>	I	-	III <sup>+</sup>	III <sup>+</sup>
<i>Sedum acre</i>	I	I <sup>+</sup>	III <sup>+</sup>	-
<i>Cetraria aculeata</i>	I	-	II <sup>+</sup>	I
<i>Galium album</i>	II <sup>2</sup>	II <sup>+3</sup>	II <sup>1</sup>	III <sup>+1</sup>
<i>Artemisia campestris</i>	I	I <sup>+</sup>	III <sup>+</sup>	I
<i>Viola tricolor</i>	II <sup>+</sup>	II <sup>+</sup>	II <sup>+</sup>	II <sup>+</sup>
<i>Astragalus arenarius</i>	I	II <sup>+2</sup>	-	-



Table 2 (continued).

1	2	3	4	5
<i>Anthyllis vulneraria</i>	.	I*	.	.
<i>Pinus sylvestris</i> A3	III <sup>+2</sup>	II+	IV <sup>+1</sup>	IV <sup>+2</sup>
<i>Betula pendula</i> A3	.	.	II*	II*
<i>Salix rosmarinifolia</i>	II <sup>-2</sup>	I+	.	III <sup>+4</sup>
<i>Empetrum nigrum</i>	.	.	II <sup>2</sup>	V <sup>+3</sup>
<i>Fragaria vesca</i>	I	.	II*	II*
<i>Taraxacum officinale</i>	I	I	I*	I
<i>Trifolium arvense</i>	I	I*	I	.
<i>Plantago lanceolata</i>	I	II*	.	I
<i>Cardamine pratensis</i>	I	.	.	I*
<i>Sorbus aucuparia</i>	I	.	.	.
<i>Geranium robertianum</i>	I	.	.	.
<i>Stellaria graminea</i>	I	I	III <sup>+1</sup>	III*
<i>Potentilla erecta</i>	I	I	II*	II*
<i>Potentilla argentea</i>	.	I	.	.
<i>Veronica chamaedrys</i>	I	.	.	I
<i>Alyssum gmelinii</i>	.	.	III <sup>+2</sup>	I
<i>Hypericum perforatum</i>	.	.	III <sup>+1</sup>	II <sup>+1</sup>
<i>Cerastium arvense</i>	.	I*	III*	II*
<i>Achillea millefolium</i>	.	II*	II*	II*
<i>Pseudoscleropodium purum</i>	.	.	II*	II <sup>i</sup>
<i>Deschampsia flexuosa</i>	.	II <sup>-2</sup>	I*	II <sup>+2</sup>
<i>Melampyrum nemorosum</i>	.	.	I*	II <sup>+1</sup>
<i>Luzula pilosa</i>	.	.	I*	II*
<i>Poa pratensis</i>	.	II*	I*	I
<i>Veronica officinalis</i>	.	.	I*	I
<i>Vicia cracca</i>	.	.	I*	I
<i>Erigeron acris</i>	.	.	II*	II*
<i>Cladonia cornuta</i>	.	IV <sup>+2</sup>	I*	I
<i>Peltigera canina</i>	.	.	I <sup>2</sup>	I
<i>Medicago falcata</i>	.	I	I*	I
<i>Polytrichum gracile</i>	.	.	I*	I
<i>Senecio jacobaea</i>	.	II*	I*	I
<i>Scleranthus perennis</i>	.	I	.	.
<i>Silene tatarica</i>	.	.	I <sup>i</sup>	I
<i>Cladonia rangiferina</i>	.	II*	II*	.
<i>Dianthus deltoides</i>	.	.	I*	.
<i>Pleurozium schreberi</i>	.	.	.	II*
<i>Dicranum polysetum</i>	.	.	.	II*
<i>Populus tremula</i> A3	.	.	.	I*
<i>Cladonia chlorophaea</i>	.	IV <sup>+2</sup>	.	I
<i>Cladonia arbuscula</i>	.	II*	.	.
<i>Cladonia furcata</i>	.	II*	.	.
<i>Cladonia phylophora</i>	.	II*	.	.
<i>Cladonia foliacea</i>	.	II*	.	I
<i>Cladonia fimbriata</i>	.	II*	.	.
<i>Cladonia floerkeana</i>	.	II*	.	.
<i>Cladonia ramulosa</i>	.	II*	.	I
<i>Cladonia subrangiformis</i>	.	II*	.	.



Table 2 (continued).

1	2	3	4	5
<i>Cladonia scabruscula</i>	.	II*	.	.
<i>Cladonia crispata</i>	.	II*	.	.
<i>Cladonia portentosa</i>	.	II*	.	.
<i>Cladonia reii</i>	.	II*	.	.
<i>Cetraria islandica</i>	.	II* <sup>-1</sup>	.	I
<i>Moneses uniflora</i>	.	.	.	I
<i>Agrostis tenuis</i>	.	I*	.	I
<i>Hylocomium splendens</i>	.	.	.	I
<i>Luzula multiflora</i>	.	.	.	I
<i>Tanacetum vulgare</i>	.	.	.	I
<i>Vaccinium myrtillus</i>	.	.	.	I

the necessary regime of humidity and temperature in the seacoast foredunes, corresponds to luxuriant, continuous cover of bryophytes and lichens as well as thick groves of *Empetrum nigrum* in palve.

3. In palve the strength of wind is reduced and irreciprocal stream is dispersed by abundantly growing *Salix rosmarinifolia*, *Salix daphnoides* shrubs, and low *Pinus sylvestris* and *Betula pendula* trees.

#### SUCCESION OF THE SEACOAST FOREST COMMUNITIES

In the Lithuanian seacoast, the *Betula pendula* communities are the first stage of forest communities formation (Table 3). They thrive in a 15–30 m wide zone in eastern part of hillocky palve and troughs. This ecological zone is discontinuous. It starts at the Avinas hill dune and stretches to Nida in the Curonian Spit. This ecological zone in continental part is also present in territories with undisturbed natural succession of communities. Comparing with other forest communities, the highest species diversity is characteristic to these communities. Here plants common to forest and grass sand communities grow the same as in stage *Empetrum nigrum* communities. In stage *Betula pendula* communities plants, characteristic to all coastal forest communities (*Deschampsia flexuosa*, *Melampyrum nemorosum*, *Empetrum nigrum*, *Luzula multiflora*, *Pseudoscleropodium purum*, *Pleurozium schreberi*, *Dicranum polysetum*) are abundant and constant, while *Calamagrostis epigejos*, *Stellaria graminea*, *Veronica officinalis*, *Jasione montana*, *Galium album*, *Rumex acetosella*, common to palve, occur rarely.

In continental part of the seacoast, the natural, regular succession of plant communities ends with this ecological zone because the major part of the territory is occupied by resort places, camps, and villages with arable fields and meadows.

There is no such anthropogenic barrier in the Curonian Spit, therefore natural succession of vegetation goes further and there are more ecological zones.

In later stages of the succession of plant communities the processes of syngensis prevail. Forest communities of different stages of succession thrive in ecological zone of hillocky palve which includes large areas and parabolic dunes (Fig. 2). The youngest parabolic dunes and derivatives of relief associated with its formation (backs, troughs, hollows) make a 1–1.5 km wide zone in the east of hillocky palve. Presently all parabolic dunes are overgrown with forest of the *Empetro nigri-Pinetum* Wojt. 1964 association. In Lithuania, these communities thrive only in a narrow zone of the Baltic seacoast. Nevertheless, they differ in age and stage of succession. The *Empetro nigri-Pinetum* subas. *typicum* communities settle in the youngest and lowest parabolic dunes and dune-slacks. This is the initial stage of formation of seacoast pinewood and next stage of sand succession towards a zonal type of vegetation. The *Empetro nigri-Pinetum* subas. *cladonietosum* communities thrive on top of higher parabolic dunes. These communities tolerate dryer conditions and distinguish by a large variety of lichens. *Jasione montana*, *Festuca sabulosa*, *Corynephorus canescens*, *Thymus serpyllum*, characteristic to grey dunes, are common in them as well as plants characteristic to forest communities. The *Empetro nigri-Pinetum* subas. *pyroletosum* communities grow on the oldest and highest parabolic dunes, which are most distant from the sea. They are the last stage of forest succession towards the climax in Lithuanian seacoast. They have denser undergrowth and undershrub comparing with other succession forest communities. *Sorbus aucuparia*, *Frangula alnus*, *Juniperus communis* are abundant in undershrub, and *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Populus tremula*, *Quercus robur*, *Betula pendula* form dense undergrowth.

Table 3.

The dominating forest communities in ecological zone of the hillocky palve, parabolic dunes, and palve near lagoon. Syntaxa: 1 – *Betula pendula* communities; 2 – *Alnus glutinosa* communities; 3 – *Empetro nigri-Pinetum* subas. typicum; 4 – *Empetro nigri-Pinetum* subas. *cladonetosum*; 5 – *Empetro nigri-Pinetum* subas. *pyroletosum*; 6 – *Quercus-Piceetum*; 7 – *Betula pendula* communities; 8 – *Alnus glutinosa* communities

Ecological zone	Hillocky palve		Parabolic dunes				Palve near lagoon	
Syntaxa	1	2	3	4	5	6	7	8
Number of relevés	15	12	11	10	30	10	13	8
Total number of species	66	59	57	45	58	29	56	59
Average number of species	19	15	17	12	17	14	18	12
Coverage (%):								
tree layer	50	71	58	72	66	51	40	64
shrub layer	9	40	4	1	7	1	8	36
herb layer	65	58	64	49	62	52	82	51
bryophyte layer	49	1	81	59	79	76	38	10
lichen layer	.	.	.	12	.	.	.	.
1	2	3	4	5	6	7	8	9
A1								
<i>Pinus sylvestris</i>	.	II <sup>+1</sup>	V <sup>1-4</sup>	V <sup>2-4</sup>	V <sup>1-4</sup>	V <sup>2</sup>	.	I
<i>Alnus glutinosa</i>	.	V <sup>2-4</sup>	.	.	.	.	.	V <sup>1-5</sup>
<i>Betula pendula</i>	.	III <sup>+3</sup>	.	.	.	.	.	V <sup>+2</sup>
<i>Picea abies</i>	.	.	.	.	.	II <sup>1-2</sup>	.	I
A2								
<i>Betula pendula</i>	V <sup>2-3</sup>	II <sup>+1</sup>	III <sup>+3</sup>	II <sup>+</sup>	III <sup>+3</sup>	III <sup>+</sup>	V <sup>2-4</sup>	I
<i>Pinus sylvestris</i>	III <sup>1-2</sup>	.	.	.	I	V <sup>1-3</sup>	IV <sup>+2</sup>	.
<i>Picea abies</i>	I <sup>+</sup>	I <sup>+</sup>	I	.	I <sup>+2</sup>	IV <sup>+1</sup>	II <sup>2</sup>	I
<i>Alnus glutinosa</i>	I	II <sup>+3</sup>	.	.	.	.	.	I
<i>Betula pubescens</i>	I <sup>+</sup>	.	.	.	.	.	I <sup>+</sup>	.
<i>Quercus robur</i>	.	.	.	.	.	V <sup>+1</sup>	.	.
<i>Sorbus aucuparia</i>	.	.	.	.	.	III <sup>+2</sup>	.	I
<i>Frangula alnus</i>	.	.	.	.	I	.	.	.
A3								
<i>Juniperus communis</i>	III <sup>+2</sup>	I	I	I	II <sup>+</sup>	III <sup>+1</sup>	IV <sup>+1</sup>	I
<i>Pinus sylvestris</i>	II <sup>+</sup>	.	I	I	I	II <sup>+2</sup>	II <sup>+1</sup>	.
<i>Betula pendula</i>	IV <sup>+2</sup>	I	.	.	.	III <sup>+</sup>	III <sup>+1</sup>	.
<i>Salix rosmarinifolia</i>	IV <sup>+2</sup>	.	II <sup>+</sup>	.	I	.	III <sup>+1</sup>	.
<i>Quercus robur</i>	I	.	I	I	II <sup>+1</sup>	III <sup>+2</sup>	I	.
<i>Sorbus aucuparia</i>	.	III <sup>+2</sup>	II <sup>+2</sup>	I	III <sup>+2</sup>	V <sup>+1</sup>	II <sup>+2</sup>	II <sup>1-2</sup>
<i>Frangula alnus</i>	.	III <sup>+2</sup>	.	.	I	I	.	I
<i>Alnus glutinosa</i>	I	II <sup>1-3</sup>	.	.	.	.	I	II <sup>+1</sup>
<i>Picea abies</i>	.	.	.	I	I	II <sup>+</sup>	.	II <sup>+</sup>
<i>Populus tremula</i>	I	.	II <sup>+3</sup>	.	I	.	I	.
<i>Betula pubescens</i>	.	.	I	.	I	.	.	.
<i>Salix aurita</i>	I	.	.	.	.	.	I	.
<i>Sambucus racemosa</i>	.	.	.	.	.	.	.	I
<i>Deschampsia flexuosa</i>	V <sup>1-3</sup>	III <sup>+4</sup>	V <sup>1-3</sup>	V <sup>+4</sup>	V <sup>+4</sup>	V <sup>+2</sup>	V <sup>+3</sup>	III <sup>+1</sup>
<i>Melampyrum nemorosum</i>	V <sup>+4</sup>	I	V <sup>+3</sup>	V <sup>+3</sup>	V <sup>+3</sup>	V <sup>2-3</sup>	V <sup>+3</sup>	II <sup>+</sup>
<i>Pleurozium schreberi</i>	V <sup>1-3</sup>	II	V <sup>1-3</sup>	III <sup>+4</sup>	V <sup>+4</sup>	V <sup>1-3</sup>	V <sup>+3</sup>	II <sup>+2</sup>
<i>Carex arenaria</i>	III <sup>+2</sup>	II <sup>+1</sup>	IV <sup>+2</sup>	V <sup>+3</sup>	IV <sup>+2</sup>	I	III <sup>+2</sup>	II <sup>+2</sup>
<i>Dicranum polysetum</i>	III <sup>1+</sup>	I	V <sup>+2</sup>	V <sup>+1</sup>	IV <sup>+2</sup>	V <sup>+</sup>	II <sup>+1</sup>	I
<i>Pseudoscleropodium purum</i>	III <sup>1+</sup>	.	V <sup>+3</sup>	IV <sup>+3</sup>	V <sup>+3</sup>	V <sup>1-3</sup>	V <sup>+3</sup>	I

Table 3 (continued).

1	2	3	4	5	6	7	8	9
<i>Empetrum nigrum</i>	IV <sup>1-4</sup>	.	V <sup>+3</sup>	.	IV <sup>+4</sup>	V <sup>+1</sup>	IV <sup>+4</sup>	I
<i>Luzula multiflora</i>	III <sup>+</sup>	.	V <sup>+</sup>	I	II <sup>+</sup>	I	II <sup>+</sup>	.
<i>Vaccinium myrtillus</i>	II <sup>+</sup>	.	IV <sup>+1</sup>	I	IV <sup>+2</sup>	V <sup>1-4</sup>	I	I
<i>Hylocomium splendens</i>	III <sup>+3</sup>	.	II <sup>+2</sup>	I	III <sup>+2</sup>	V <sup>+3</sup>	II <sup>+</sup>	.
<i>Trientalis europaea</i>	.	I	IV <sup>+</sup>	II <sup>+1</sup>	III <sup>+1</sup>	V <sup>+</sup>	II <sup>+1</sup>	V <sup>+</sup>
<i>Dryopteris carthusiana</i>	.	V <sup>+3</sup>	III <sup>+</sup>	.	II <sup>+2</sup>	III <sup>+</sup>	II <sup>+1</sup>	V <sup>+1</sup>
<i>Luzula pilosa</i>	I	I	III <sup>+1</sup>	.	III <sup>+1</sup>	V <sup>+1</sup>	I	II <sup>+</sup>
<i>Vaccinium vitis-idaea</i>	II <sup>+</sup>	.	III <sup>+2</sup>	.	IV <sup>+2</sup>	V <sup>+2</sup>	II <sup>+</sup>	I
<i>Majanthemum bifolium</i>	.	I	II <sup>+</sup>	I	II <sup>+2</sup>	V <sup>+2</sup>	I	II <sup>+</sup>
<i>Poa pratensis</i>	II <sup>+2</sup>	II <sup>+</sup>	I	.	I	.	III <sup>+1</sup>	III <sup>+</sup>
<i>Agrostis tenuis</i>	III <sup>+3</sup>	II <sup>+1</sup>	II <sup>+</sup>	I	I	.	III <sup>+3</sup>	II <sup>+2</sup>
<i>Anthoxanthum odoratum</i>	IV <sup>+1</sup>	I	II <sup>+</sup>	I	I	I	II <sup>+1</sup>	II <sup>+</sup>
<i>Hieracium umbellatum</i>	III <sup>+</sup>	.	I	III <sup>+1</sup>	I	.	IV <sup>+1</sup>	.
<i>Stellaria graminea</i>	III <sup>+</sup>	I	.	I	I	.	II <sup>+</sup>	I
<i>Veronica officinalis</i>	III <sup>+</sup>	.	.	.	.	.	III <sup>+</sup>	.
<i>Calamagrostis epigejos</i>	II <sup>+1</sup>	.	.	.	.	.	II <sup>+1</sup>	.
<i>Jasione montana</i>	II <sup>+</sup>	.	.	II <sup>+1</sup>	I	.	I	.
<i>Galium album</i>	II <sup>+</sup>	.	.	.	.	.	.	.
<i>Rumex acetosella</i>	II <sup>+</sup>	II <sup>+</sup>	I	.	I	.	II <sup>+</sup>	I
<i>Fragaria vesca</i>	II <sup>+2</sup>	.	.	.	.	.	I	I
<i>Veronica chamaedrys</i>	II <sup>+</sup>	I	.	.	.	.	II <sup>+1</sup>	II <sup>+</sup>
<i>Hypericum perforatum</i>	II <sup>+</sup>	.	.	.	.	.	II <sup>+2</sup>	.
<i>Achillea millefolium</i>	II <sup>+2</sup>	.	.	.	.	.	II <sup>+1</sup>	.
<i>Moneses uniflora</i>	II <sup>+</sup>	.	II <sup>+</sup>	I	I	I	I	.
<i>Stellaria media</i>	II <sup>+</sup>	IV <sup>+2</sup>	.	.	.	.	.	IV <sup>+2</sup>
<i>Calamagrostis arundinacea</i>	I	.	.	.	.	.	.	.
<i>Carex nigra</i>	I	I	.	.	I	.	I	I
<i>Climacium dendroides</i>	I	.	.	.	.	.	.	.
<i>Dicranum scoparium</i>	I	.	I	II <sup>1-2</sup>	II <sup>+1</sup>	.	.	.
<i>Galium verum</i>	I	.	.	.	.	.	.	.
<i>Geranium robertianum</i>	I	II <sup>+1</sup>	.	.	.	.	.	III <sup>+</sup>
<i>Holcus lanatus</i>	I	.	.	.	.	.	.	.
<i>Juncus balticus</i>	I	.	.	.	.	.	.	.
<i>Juncus effusus</i>	I	II <sup>+</sup>	.	.	.	.	I	I
<i>Pilosella officinarum</i>	I	.	.	.	.	.	.	.
<i>Pyrola rotundifolia</i>	I	.	.	.	.	.	I	.
<i>Polytrichum commune</i>	I	.	I	I	I	II <sup>+</sup>	.	.
<i>Urtica dioica</i>	I	IV <sup>+2</sup>	.	.	.	.	.	IV <sup>+1</sup>
<i>Vicia cracca</i>	I	.	.	.	.	.	I	.
<i>Viola canina</i>	I	.	.	.	.	.	I	.
<i>Calluna vulgaris</i>	.	.	I	.	I	V <sup>+1</sup>	.	.
<i>Polygonatum multiflorum</i>	.	I	I	I	I	.	.	I
<i>Pyrola chlorantha</i>	.	.	I	I	II <sup>+</sup>	.	.	.
<i>Linnaea borealis</i>	.	.	I	.	II <sup>+2</sup>	II <sup>+</sup>	.	.
<i>Oxalis acetosella</i>	.	I	I	.	I	I	I	II <sup>+1</sup>
<i>Lycopodium annotinum</i>	.	.	I	.	I	I	.	.
<i>Galium album</i>	.	.	I	I	I	.	I	.
<i>Moehringia trinervia</i>	.	V <sup>+1</sup>	I	I	I	.	.	V <sup>+1</sup>
<i>Festuca sabulosa</i>	.	.	I	II <sup>+1</sup>	I	.	.	.
<i>Taraxacum officinale</i>	.	.	I	.	I	.	.	.
<i>Cladonia mytis</i>	.	.	.	III <sup>+2</sup>	.	.	.	.



Table 3 (continued).

1	2	3	4	5	6	7	8	9
<i>Cetraria islandica</i>	-	-	-	III <sup>+1</sup>	-	-	-	-
<i>Cladonia cristata</i>	-	-	-	II <sup>1-2</sup>	-	-	-	-
<i>Cladonia chlorophaea</i>	-	-	-	II <sup>2</sup>	-	-	-	-
<i>Cladonia arbuscula</i>	-	-	-	I	-	-	-	-
<i>Cetraria aculeata</i>	-	-	-	I	-	-	-	-
<i>Ceratodon purpureus</i>	-	-	-	I	-	-	-	-
<i>Cladonia rangiferina</i>	-	-	-	I	-	-	-	-
<i>Cladonia aporinquata</i>	-	-	-	I	-	-	-	-
<i>Thymus serpyllum</i>	-	-	-	I	I	-	-	-
<i>Chamaerion angustifolium</i>	-	-	-	I	-	-	-	-
<i>Rubus idaeus</i>	-	III <sup>1-4</sup>	-	-	I	-	-	III <sup>+3</sup>
<i>Galium boreale</i>	-	III <sup>+</sup>	-	-	I	-	-	II <sup>+2</sup>
<i>Plagiothecium umbellatum</i>	-	-	-	-	I	-	-	-
<i>Potentilla erecta</i>	-	-	-	-	I	-	I	-
<i>Platanthera bifolia</i>	-	-	-	-	I	-	-	-
<i>Neottia nidus-avis</i>	-	-	-	-	I	-	-	-
<i>Astragalus arenarius</i>	-	-	-	-	I	-	-	-
<i>Dryopteris filix-mas</i>	-	-	-	-	I	-	-	-
<i>Rhytidadelphus triquetrus</i>	-	-	-	-	I	I	-	-
<i>Racomitrium canescens</i>	-	-	-	-	I	-	-	I
<i>Leucobryum glaucum</i>	-	-	-	-	I	II <sup>+1</sup>	-	-
<i>Sphagnum squarrosum</i>	-	-	-	-	-	III <sup>+</sup>	-	-
<i>Dryopteris linneana</i>	-	-	-	-	-	I	-	-
<i>Ptilium crista-castrensis</i>	-	-	-	-	-	I	-	-
<i>Pteridium aquilinum</i>	-	-	-	-	-	I	-	-
<i>Climacium dendroides</i>	-	-	-	-	-	-	II <sup>+1</sup>	-
<i>Phleum pratense</i>	-	-	-	-	-	-	I	-
<i>Molinia caerulea</i>	-	-	-	-	-	-	I	-
<i>Stellaria holostea</i>	-	I	-	-	-	-	I	-
<i>Phragmites australis</i>	-	I	-	-	-	-	I	I
<i>Calamagrostis canescens</i>	-	III <sup>2-4</sup>	-	-	-	-	I	II <sup>+2</sup>
<i>Mycelis muralis</i>	-	III <sup>+1</sup>	-	-	-	-	-	II <sup>+</sup>
<i>Lysimachia vulgaris</i>	-	II <sup>+1</sup>	-	-	-	-	-	II <sup>+</sup>
<i>Scutellaria galericulata</i>	-	III <sup>+1</sup>	-	-	-	-	-	II <sup>+1</sup>
<i>Crepis paludosa</i>	-	I	-	-	-	-	-	II <sup>+</sup>
<i>Athyrium filix-femina</i>	-	I	-	-	-	-	-	II <sup>1-2</sup>
<i>Geum rivale</i>	-	I	-	-	-	-	-	I
<i>Impatiens noli-tangere</i>	-	I	-	-	-	-	-	I
<i>Equisetum arvense</i>	-	I	-	-	-	-	-	I
<i>Stellaria alsine</i>	-	I	-	-	-	-	-	I
<i>Naumburgia thyrsiflora</i>	-	I	-	-	-	-	-	-
<i>Circaea intermedia</i>	-	I	-	-	-	-	-	-
<i>Epilobium hirsutum</i>	-	I	-	-	-	-	-	-
<i>Lamium purpureum</i>	-	I	-	-	-	-	-	-
<i>Chelidonium majus</i>	-	-	-	-	-	-	-	I
<i>Iris pseudacorus</i>	-	-	-	-	-	-	-	I
<i>Anthriscus sylvestris</i>	-	-	-	-	-	-	-	I
<i>Aegopodium podagraria</i>	-	-	-	-	-	-	-	I

Moving from the West to the East, in forest communities the following structural succession occurs (Table 3):

1. In the layers of tree stand of primary forest communities A1 and A2 *Pinus sylvestris* is abundant. There is no underwood. In later succession stages in A1 layer *Pinus sylvestris* becomes thinner, and in A2 *Picea abies*, *Betula pendula* start to grow; *Sorbus aucuparia*, *Frangula alnus* start forming the underwood.

2. In herb layer, plants of wide ecological range that have been dominant in primary stages are replaced by species characteristic to forest communities (*Deschampsia flexuosa*, *Melampyrum nemorosum*, *Luzula multiflora*, *Trifolium europaeum*, *Majanthemum bifolium*).

3. Bryophyte layer thickens (*Pleurozium schreberi*, *Pseudoscleropodium purum*, *Hylocomium splendens*, *Ptilium crista-castrensis*, *Dicranum polysetum*), leaf-litter forms, the amount of humus increases.

The oldest seacoast forests, which have reached climax stage, thrive on the oldest parabolic dunes near Juodkrantė. These communities are the result of a change of naturally forming seacoast vegetation. Tree layer is composed of high (over 30 m) and old *Pinus sylvestris* as well as lower (up to 15–20 m) *Picea abies*. *Quercus robur* is often present, *Betula pendula* – occasionally. Undergrowth is very dense. *Sorbus aucuparia*, *Frangula alnus*, *Juniperus communis* are quite abundant. There are a lot of small (up to 1 m height) *Quercus robur*, *Picea*

*abies*, *Pinus sylvestris* trees in the undergrowth. Trees of different layers overlap and their coverage is up to 90 %. The number of species in the herb layer is not high comparing with other forest communities, nevertheless they grow in large overlapping thickets. Herb layer as well as tree layer is continuous. A distinctly separate layer of mosses is formed under the herb layer. It consists of *Pseudoscleropodium purum*, *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum polysetum*, *Sphagnum squarrosum*.

#### SUCCESSION OF THE SAND VEGETATION ON THE GREAT DUNE RIDGE

In the Curonian Spit on the great dune ridge vegetation successions are induced and supported by abiotic factors, therefore, here, like on the seacoast foredunes, the process of endoeogenesis occurs. As the influence of the lagoon upon the land vegetation is considerably slighter than that of the sea, on the great dune ridge (Fig. 3) not the initial psammophytic communities but already xerophytic *Violo-Corynephorum canescens* (Böcher 1941) Westhoff et al. 1946 communities of stabilised sand form. The main difference is that in foredunes the coverage of communities, species number, stabilisation of sand, the amount of humus vary according to prevailing western winds, while in great dune ridge



Fig. 3. Distribution of the sand vegetation in cross-section, in the Curonian Spit near Arkliai horn (97; 98; 99; 100; 101; 102/103; 104; 105; 106; 107; 108 forest blocks). 1 – single *Cakile maritima*, *Salsola kali*, *Honckenya peploides* tussocks; 2 – *Leymo-Ammophiletum subas. typicum* and *Leymo-Ammophiletum subas. petasitetosum*; 3 – *Leymo-Ammophiletum subas. festucetosum sabulosae*; 4 – *Leymo-Ammophiletum subas. artemisietosum*; 5 – *Carex arenaria* stage communities; 6 – *Helichryso-Jasionetum*; 7 – *Empetrum nigrum* stage communities; 8 – *Betula pendula* stage communities; 9 – *Alnus glutinosa* stage communities; 10 – *Empetrum nigri-Pinetum subas. typicum*; 11 – *Empetro nigri-Pinetum subas. cladonietosum*; 12 – *Empetro nigri-Pinetum subas. pyroletosum*; 13 – *Violo-Corynephorum canescens*



zone these characteristics change from East to West. The influence of the lagoon on land vegetation is weaker than of the sea, thus in the zone of moving dunes of the great dune ridge *Violo-Corynephorum canescens* communities of stabilised sand, rather than initial communities of white dunes, form. They are characterised by the inheritance to xerophytic ecotopes, but the structure and species variety correspond to conditions of permanent humidity deficit. The edificators of the communities (*Corynephorus canescens*, *Festuca polesica*, *Festuca sabulosa*) are typical xerophytes. Abundantly growing mosses and lichens are very important stabilising components. They cover almost all the sandy area, keep water vaporizing from the surface, store precipitation and distribute it evenly. Thus favourable microclimate for establishment of weak competitors lacking special adaptation forms.

In the upper part of western slope of the great dune ridge there are many sand hummocks with *Ammophila arenaria*, *Calamagrostis epigejos*, and *Festuca arenaria* as well as plant-free deflation sand hollows. On the top of the great dune ridge dominating western wind is complemented by eastern one (GUDELIS, 1998); therefore, free sand, not strengthened by plants, is carried in all directions. Plant communities of several succession stages are situated in this part of the great dune ridge. *Leymo-Ammophiletum* subas. *typicum*, *Violo-Corynephorum canescens*, and *Empetrum nigrum*. *Betula pendula* stages are located mosaically in small overlapping areas.

In a zone of moving dunes, the eastern, very steep slope of the great dune ridge descends right into the lagoon. Rising of water level in the Curonian Lagoon washes out the sand, and a lot of sand landslips occur.

At present two-thirds of the great dune ridge are occupied by the *Pinus mugo* communities (Fig. 3). They are made artificially, in order to stop the moving sand. *Pinus mugo* is an introduced species in the Lithuanian seacoast (DAUJOTAS, 1958). Planting of the great dune ridge was carried out between 1811 and 1904 (BUČAS, 1998). At present the number of species in the *Pinus mugo* communities located on the great dune ridge is not high; *Pinus mugo* dominates. The trees are of 2–3 m height, branching almost from the ground, their matted branches form dense impassable thickets which totally stop the wind. Their flat and widely spread roots help to keep and accumulate the necessary amount of water in sand. Mosses (*Pleurozium schreberi*, *Pseudoscleropodium purum*, *Dicranum scoparium*, *Polytrichum piliferum*) and lichens (*Cladonia mitis*, *Cladonia glauca*, *Cladonia gracilis*, *Cetraria aculeata*, *Cetraria islandica*) grow between *Pinus mugo*. There are almost no graminaceous plants. Solitary tufts of *Deschampsia flexuosa* are dispersed,

and in some places *Melampyrum nemorosum*, *Jasione montana*, *Carex arenaria* grow.

Palve near the lagoon does not make a continuous zone (Fig. 3). It is located beyond the part of the great dune ridge with *Pinus mugo* thickets and best developed at the Grobštas, Bulvikis, and Žirgai horns. A succession of plant communities in palve near the lagoon is quite similar to the one next to the sea, only the direction of change differs. The *Helichryso-Jasionetum* communities near the sea from West to East are replaced by the *Empetrum nigrum* and *Betula pendula* communities. Near the lagoon the zone of *Betula pendula* and *Alnus glutinosa* communities thrive just beside the eastern part of the great dune ridge with *Pinus mugo* thickets. Further, the associations of *Helichryso-Jasionetum* community with *Empetrum nigrum* and intervening fragments of *Violo-Corynephorum canescens* grow.

The beach of the lagoon is discontinuous. Usually there are 3–6 m wide sand beaches only at horns of the Spit and in bays between them. The *Leymo-Ammophiletum* subas. *typicum* and *Leymo-Ammophiletum* subas. *petasitetosum* communities thrive here, while in damp, permanently flooded parts, dense monodominant *Phragmites australis* overgrowths are abundant. Seasonal water level fluctuations in the lagoon as well as spring crushing of trash-ice mechanically destroy the existing communities, hence the latter always survive in initial stage of establishment.

## WHICH COMMUNITIES FINISH THE SEACOAST SANDY PLANT SUCCESSION

Investigations of the autogenic succession of seacoast plant communities from the spatial point of view revealed that this process starts from monodominant groves of *Ammophila arenaria*, *Calamagrostis epigejos*, *Leymus arenarius*, and *Honckenya peploides*. They form accumulative sand moulds in the western part of seacoast beach. However, the determination and naming of final stage (climax) communities remain problematic. Species composition and structure is an obvious reflexion of edaphic conditions due to peculiarities of relief. Studying reasons of the development of present communities as well as predicting trends of their subsequent change, it is necessary to analyse the composition and features of soil, geomorphologic structures and their impact to plant communities. Individual morphologic and physiological distinctions of certain community-forming species are very important as well as ability to compete, to inhabit free ecological niches, and to survive.

Aeolian sand is the main and prevailing type of soil on the whole seacoast of Lithuania. It is very poor (0.001–0.04 %) in nutrients available for plants ( $N_{\text{tot}}$ ,  $P_2O_5$ ,  $K_2O$ ), thereby produces no impact for the succession of plant community. It is worthwhile to analyze thoroughly pH of the soil, amount of humus, regularities of plant species number change and homogeneity of communities as well as correlation between them.

The pH of beach and white dune sand is close to neutral (6.4–6.8). It decreases to pH 4.6–5.2 getting further from the sea – in the palve (except for *Empetrum nigrum* stage communities, where pH remains 6.2), in the hillocky palve pH 4.0, and in forest communities acid soil dominates (pH 4.0–4.2) (Fig. 4).

Increase of the amount of humus correlates with the acidification of the soil (Fig. 5). Humus is almost absent on foredunes of the seaside (0.01–0.03 %). The amount of humus varies between 0.34–0.64 % in all herb communities and highly increases in forest communities located

after *Betula pendula* communities (1.20–4.84 %). The highest (5.4 %) humus amount was revealed in the *Alnus glutinosa* communities of waterlogged palve and palve by the lagoon.

The acidity of soil and the amount of humus vary gradually shifting from one ecological zone to another, while the number of species composing communities changes sharply (BIGON, 1989) (Fig. 6). In the first succession stages of *Leymo-Ammophiletum* subas. *typicum*, *Leymo-Ammophiletum* subas. *petasitetosum*, *Leymo-Ammophiletum* subas. *festucetosum sabulosae*, *Leymo-Ammophiletum* subas. *artemisietosum* the number of species composing the communities gradually increases, and new species settle after the negative influence of

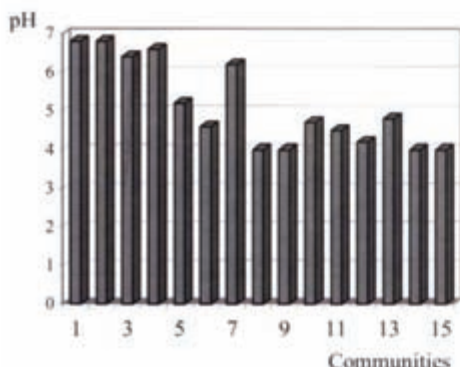


Fig. 4. Soil pH values of investigated plant communities in the Curonian Spit

Communities: 1 – *Leymo-Ammophiletum arenariaea* subas. *typicum*; 2 – *Leymo-Ammophiletum arenariaea* subas. *petasitetosum*; 3 – *Leymo-Ammophiletum arenariaea* subas. *festucetosum sabulosae*; 4 – *Leymo-Ammophiletum arenariaea* subas. *artemisietosum*; 5 – *Carex arenaria* stage communities; 6 – *Helichryso-Jasionetum*; 7 – *Empetrum nigrum* stage communities; 8 – *Betula pendula* stage communities in the seacoast palve; 9 – *Empetro nigri-Pinetum* subas. *typicum*; 10 – *Empetro nigri-Pinetum* subas. *cladonietosum*; 11 – *Empetro nigri-Pinetum* subas. *pyroletosum*; 12 – *Betula pendula* stage communities of the lagoon coastal zone palve; 13 – *Quercus-Piceetum*; 14 – *Alnus glutinosa* stage communities of the seacoast palve; 15 – *Alnus glutinosa* stage communities of the lagoon coastal zone palve

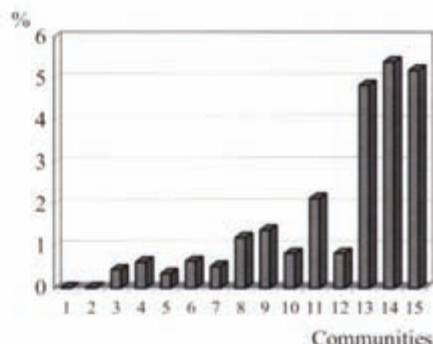


Fig. 5. Amount of humus in the soil of plant communities in the Curonian Spit. Numbers of communities as in Fig. 4

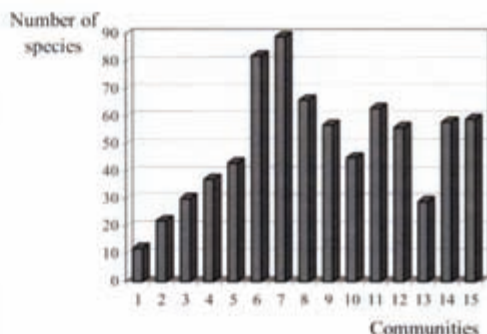


Fig. 6. Number of species in plant communities in the Curonian Spit. Numbers of communities as in Fig. 4



abiotic factors. In the next succession stage, in the ecological zone of palve, in communities of the *Helichryso-Jasionetum* association and stage *Carex arenaria* communities, the number of species increases twice because plants characteristic to grey dunes grow together with psammophytes of white dunes. The highest number of species is in the *Empetrum nigrum* stage communities. Spatially and temporarily they occupy ecotonic position between two different types of vegetation – sand and forest communities. Comparing the stage *Empetrum nigrum* community and the primary *Betula pendula* forest community, significant decrease of species number is evident; while in further succession of forest communities fluctuations of species number are insignificant. Second evident decrease of the species number is in the old-forest communities by Juodkrantė. For a long time ecologists from different countries (HORN, 1981; KORMONDY, 1992; MAY, 1973; ODUM, 1986; WITTEKER, 1980) as well as geobotanists (NATKEVIČAITĖ-IVANAUSKIENE, 1983; WOJTEWSKI, 1993; FISCHER, 1998; PIOTROWSKA, 1965) discuss whether the abundance of species number in communities show they have reached the climax stage. There is also an opinion (BIGON, 1989) that this is an initial stage or adaptation to variety of edaphic conditions. In order to solve this problem as well as validate it, the degree of homogeneity – one of the characteristic parameters of community – was analyzed (Fig. 7). This parameter is calculated employing statistical methods and is expressed by the Koch coefficient.

In the succession series of seacoast vegetation the homogeneity of communities is inversely proportional to the number of species (Fig. 8). In other succession stages the homogeneity decreases in inverse proportion to

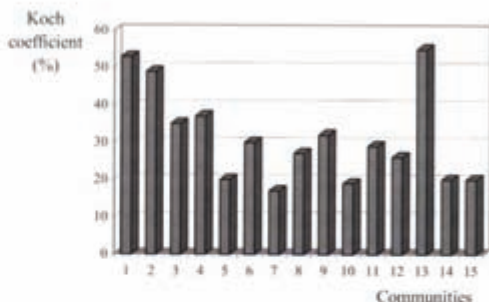


Fig. 7. The homogeneity (Koch coefficient) of plant communities in the Curonian Spit. Numbers of communities as in Fig. 4

the increase of species number. The homogeneity is minimal in the stage *Empetrum nigrum* communities that are distinguished by the highest number of plant species. In forest communities, stretching behind them, the homogeneity increases again and reaches maximum in old-forest communities of Juodkrantė. In the succession sequence of the Lithuanian seacoast vegetation, from the point of view of community homogeneity, two maximums occur: in the communities of the first and the last succession stages. While considering these communities singly, as the objects of separate scientific interest, it becomes evident that they are not similar. Only the age of these communities is similar, however, there is no a single common plant species, and they belong to different vegetation types.

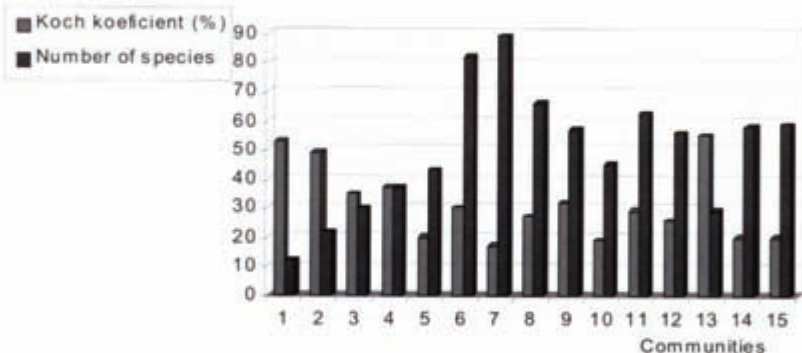


Fig. 8. Correlation between the number of species and the homogeneity of the investigated communities in the Curonian Spit. Numbers of communities as in Fig. 4



The *Leymo-Ammophiletum arenariae* communities, formed on the protective dunes of the Lithuanian sea-coast, with or without human help, are the result of the sea impact on the continental vegetation. Therefore, due to the strongest impact of factors related to the sea, communities nearest to the sea are the most homogeneous, and the combination as well as number of the composing species are optimal. According to the polyclimax theory developed by WITTAKER (1980), these communities reflect the edaphic climax.

The direct influence of the sea on the coastal vegetation decreases landward as well as the number of psammophytic species in communities, while the number of xerophytes and mesophytes related to the zonal type of vegetation (mixed forest) increases. In eastern part of palve, where the *Empetrum nigrum* stage communities are located, essential changes occur: the character of the influence of abiotic factors alter, species groups characteristic to two types of vegetation mix. Therefore, species number in this zone is the highest, but the degree of homogeneity is the lowest. Further succession in forest communities turns towards the formation of mixed forest – a zonal type of vegetation. The second maximum of homogeneity is the old-forest community near Juodkrantė, which, according to KLEMENS (1930) monoclinal theory, corresponds to the type of vegetation of our climatic zone.

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## LIETUVOS PAJŪRIO SMĖLYNŲ AUGALIJOS SUKCESIJA

Jolanta STANKEVIČIŪTĖ

Santrauka

Lietuvos pajūryje smėlynų augalijos sukcesija vyksta augalų bendrijų specializacijos išnaudojimo ir keisti esamas edafines sąlygas linkme. Ilgainiui besikeičiančios bendrijos įgauna stabilią struktūrą, kuri nepriklauso nuo pradinio varianto. Šiame darbe nagrinėjama Lietuvos pajūryje esančių, išsidėsčiusių vakarų–rytų kryptimi augalų bendrijų sukcesija ir smėlynų augalijos kitimo dėsninumu.

Jūros paplūdimyje trumpalaikius sąžalynus sudaro tik prisitaikę augti birame smėlyje augalai: *Ammophila arenaria*, *Honckenya peploides*, *Leymus arenarius*, *Calamagrostis epigejos*. Tolstant nuo jūros, keičiantis reljefo formoms, sukcesiją palaikančios jėgos persiskirsto: susilpnėja visų abiotinių veiksnių įtaka arba jos visiškai nelieta, dėl to padaugėja augalų rūšių, diferencijuojasi augalijos ardai ir padidėja projekcinis padengimas.

Skirtingose pajūrio apsauginio kopagūbrio dalyse išsidėsčiusios bendrijos atlieka skirtingas funkcijas: vakariniame šlaite esančias mažarūšes *Leymo-Ammophiletum* subas, *typicum* ir *Leymo-Ammophiletum* subas, *petasitetosum* bendrijas sudaro psamofitai, kurių funkcija – sulaikyti judrų smėlį, ant pajūrio apsauginio kopagūbrio viršaus esančias *Leymo-Ammophiletum* subas, *festucetosum sabulosae* bendrijų iš dviejų lygmenų sudarytas žolynas sumažina temperatūros ir drėgmės svyravimus, o rytiniame šlaite plytinčiose divardėse (žolių ir samanų ardai) *Leymo-Ammophiletum* subas, *artemisetosum* pradeda formuotis humusai.

Palvėje nešamą smėlį sulaiko gausiai augantys *Carex arenaria*, *Corynephorus canescens*, *Festuca sabulosa*,

*Festuca polesica*, pavieniai, tankūs *Empetrum nigrum* guotai, ištisinė samanų ir kerpių danga. Vėjo stiprumą ir vienkryptį srautą čia nuslopiną ir išsklaido gausūs *Salix rosmarinifolia*, *Salix daphnoides* krūmai bei žemi *Pinus sylvestris* ir *Betula pendula* medžiai.

Miško bendrijose iš vakarų į rytus vyksta tokios medyno struktūros kaitos. Pirminėse miško bendrijose A1 ir A2 medyno arduose gausiai auga *Pinus sylvestris*. Toliau vykstant sukcesijai A1 arde *Pinus sylvestris* retėja, o A2 dar pradeda augti *Picea abies*, *Betula pendula*, formuojasi trakas iš *Sorbus aucuparia*, *Frangula alnus*. Žolių arde vyračiusius plačios ekologinės amplitudės augalus keičia būdingi miško bendrijoms (*Deschampsia flexuosa*, *Melampyrum nemorosum*, *Luzula multiflora*, *Trientalis europaea*, *Majanthemum bifolium*), tankėja samanos, formuojasi miško paklotė, didėja humuso kiekis.

Nustatyta, kad Lietuvos pajūryje smėlynų augalijos edafinį klimaksą atitinka *Leymo-Ammophiletum arenariae* Br.-Bl. et De Leeuw 1936, o klimatinį klimaksą – *Quercus-Piceetum* Mat. et Pol. 1955 bendrijos. Nustatytos pagrindinius sukcesijos etapus sudarančios bendrijos: *Leymo-Ammophiletum arenariae* Br.-Bl. et De Leeuw 1936, *Violo-Corynephorum canescens* (Böcher 1941) Westhoff et al. 1946, *Helichryso-Jasionetum* Libbert 1940, *Empetro nigri-Pinetum* Wojt. 1964 bei pereinamosios *Carex arenaria*, *Betula pendula*, *Alnus glutinosa* stadijos.

# NEMUNAS LOWER REACHES

## Introduction

The Nemunas Delta is the region 48 km to the East above the Nemunas mouth, where the river branches off to Rusnė and Gilija and wide floodplain turns gradually into flat lowland in the West. A unique landscape of the delta includes many of distributaries (Atmata, Pakalnė, Skatulė, Skirvytė, Vytinė, Vorusnė) of the Nemunas River, Krokų Lanka Lake, Rusnė Island, Curonian Lagoon avandelta, mire complexes, waste areas of polders with fertile flooded meadows, etc.

During the last 6 000 years, the Nemunas Delta has been slowly formed of the silt (sand and sludge) brought by the Nemunas, Minija and other rivers. Due to the constant accumulation of alluvial silt, the delta had slowly risen up by expanding towards the Curonian Lagoon. Over time the silt filled-up some river branches, forming small lakes, also known as oxbow lakes. The only lagoon lake in Lithuania – Krokų Lanka was also formed in a similar manner.

The Nemunas Delta is one of the few places in Europe where rather severe flooding takes place each year. As snow begins to melt at the end of winter, water





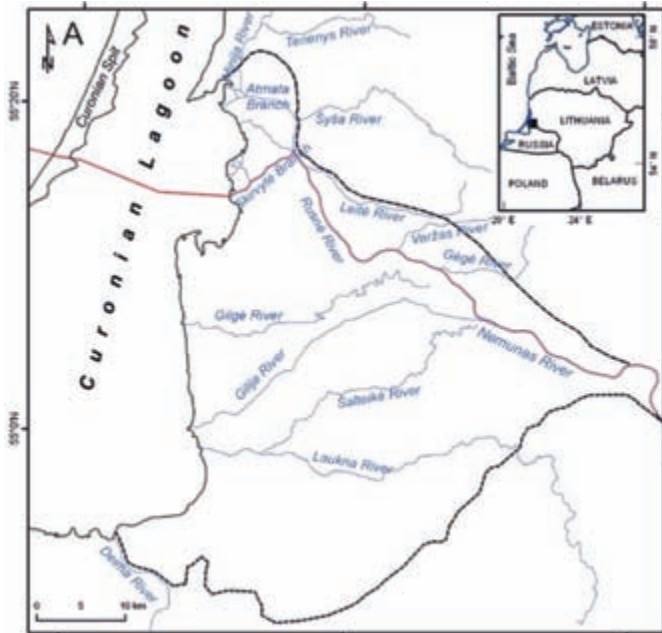


levels rise and large areas up to 400 km<sup>2</sup> get flooded. Most often flooding starts at the end of March, and continues for 2–3 weeks and sometimes even longer.

This region is famous worldwide for its unique and rich nature. In 1993, the Nemunas Delta was included in the list of wetlands of international importance and is protected under Ramsar Convention. Since 1998, it has been a Baltic Sea Protected Area designated by Helsinki Commission (HELCOM), and since 2004 – a part of the network of protected areas of European importance (Natura 2000).

## Geographical location

According to V. Gudelis (1987), the starting area point for the continental Nemunas Delta is the place, where the mouth divides into two main branches: the right one – Rusnė and the left one – Gilija. The Gilija flows through the Kaliningrad region (Russia) to the Curonian Lagoon. The second branch of the Rusnė River, after its embranchment, turns to the north–west and is named the Atmata. The Atmata River flows around Rusnė Island and near Uostadvaris it joins the Minija River and 3 km further downstream it flows into the Curonian Lagoon. The Atmata since the 19th century has been maintained for shipping purposes, the banks have been reinforced and its mouth regularly dredged (Pupienis et al., 2012).

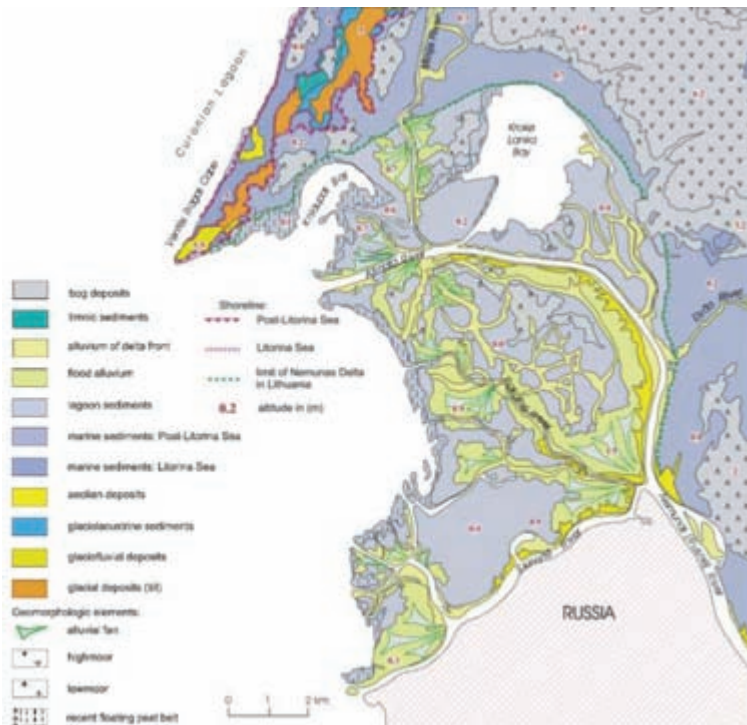


Location of the Nemunas River Delta and its boundary after V. Gudelis (1987).  
(From Pupienis et al., 2012).

## Geology and geomorphology

The Nemunas Delta has been deposited during different stages of the Baltic Sea: the *Baltic Ice Lake*, *Ancylus Lake*, *Litorina* and *Post-Litorina Sea* (Bitinas et al., 2002). The Nemunas River has formed a complex and distinctive geomorphological body at its mouth. In the same bay a smaller delta, of the Minija River, has developed. At present, these two deltas have practically merged into a common delta named the Nemunas Delta. The flat surface of the plain, from 1.5 m above sea level at its oldest part (at Rusnė), consistently drops westwards and at the shore of the Curonian Lagoon rises only some dozens of centimetres above water level.

Formation of the delta has been and still is of cyclic character: firstly, on the bottom of the basin, sub-aqueous deposition formed a fore-delta. This delta, with further deposition, formed a shallow shoal – the delta front, which emerged above water level and formed the subaerial delta separating



Geological–geomorphological structure of the Nemunas Delta (Bitinas et al., 2002)

isolated water bodies – lagoons from the basin. This cycle was subsequently repeated: river channels branched off, flowed across the emergent part of the delta and again formed fore-deltas, and so on. At the mouths of the rivers and rivulets the depositional forms – *river-mouth islands* – appeared and in the course of time joined the main land. Individual rivulet channels turned into the bog-creeks, river meanders became *oxbow lakes*, and delta plain surfaces became channelled intermittent floods. Growing delta fans divided the lagoon into smaller closed or semi-closed basins, in which lagoon deposition continued. Later some basins, by then entirely enclosed, began to transform into bogs. The uppermost parts of the alluvial deposits were later locally modified by aeolian processes. Thus, five facies have been recognised and mapped across the recent Nemunas Delta: delta front alluvium, flood alluvium, lagoon sediments, bog deposits and aeolian deposits.

Deposition on the Nemunas Delta was rapid and the accumulation rate increased in the Middle Ages. This was associated with intensifying agriculture and associated soil erosion, and hence by increased input of sediment into the rivers. In less than a century, the coastline in some places has shifted towards the Curonian Lagoon by more than 1 km. Hence, such a rate of deposition is high enough for the present Nemunas Delta to have formed during the last 1 000–1 100 years.

## Climate

The climate of Nemunas Delta region is temperate maritime and belongs to the Seaside lowlands climatic sub-district with relatively mild winters (average air temperature in January  $-2.5^{\circ}\text{C}$ ) and moderately warm summers (in July  $17.1^{\circ}\text{C}$ ). The phenoclimatic summer season with the average air temperature above  $5^{\circ}\text{C}$  lasts for 156 days. The annual temperature average is  $7.2^{\circ}\text{C}$ . The average annual rainfall is from 750 to 800 mm/year.





## Landscape history

The anthropogenic transformation of the Nemunas Delta began in the 13<sup>th</sup> century, when the Teutonic Order, having settled down in the region, started building reinforced castles and roads. The Nemunas Delta had featured no settlements at least until 1386, and its landscape was predominated by forest and wetlands, with rivers winding in them. People, so-called *Lietuvninkai* (or *Prussian Lithuanians* originally Lithuanian language speakers, who inhabited a territory in East Prussia called *Lithuania Minor*) started to settle down the higher places by the rivers at the end of the 17<sup>th</sup> century. The economic transformation of the region took place not merely for the sake of waterways; it covered a much wider circle of interest: riverbeds were straightened, canals were excavated, and dykes were built along the rivers and around the settlements to protect them from floods. Simultaneously, the network of land roads was formed. In the 18<sup>th</sup> century, hydraulic engineering already acquired the features of the landscape adaptation to agriculture. The plague of 1709–1711 changes the ethnic composition of delta population. The deserted homesteads of the former residents were offered to colonist from Germany, Austria



and other countries. New colonists brought more modern farming culture and new growing plants (potatoes, tobacco).

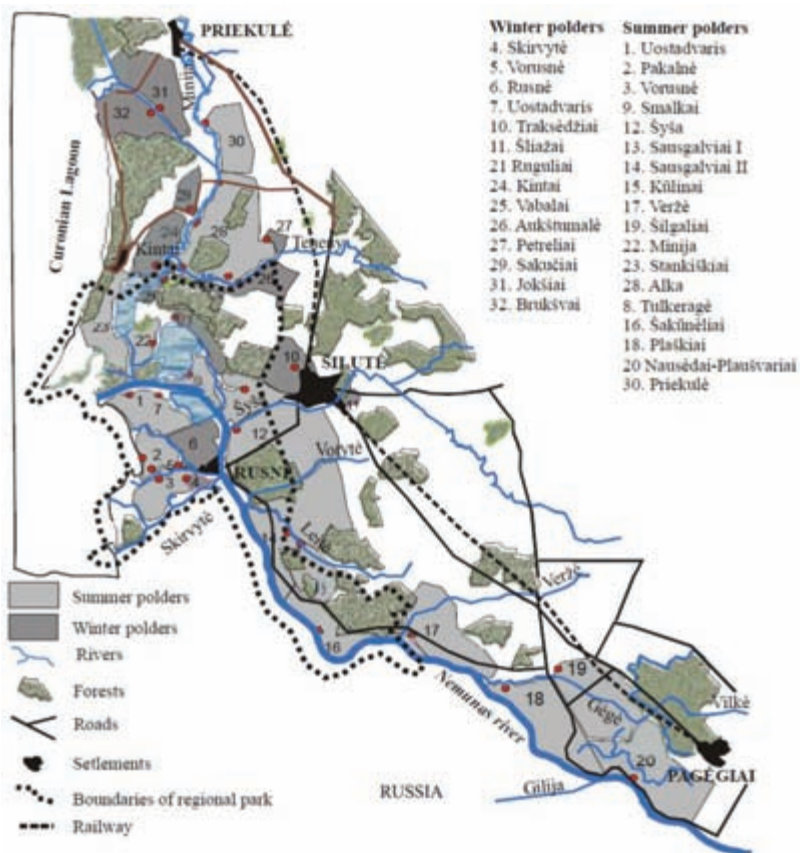
In this region, powerful annual floods and ice-drifts shape the landscape. The floods are changing the landscape, fertilizing meadows, revitalizing nature after winters and sometimes even carry timber. Such natural conditions determined distinctive lifestyle, customs, trades, and farming traditions in the Nemunas Delta. This region has been home for unique, rather closed communities of fishermen, gardeners, grassland and wetland farmers. Fishermen lived near the water, while wetland farmers stayed around mires, and those making a living of forests lived in local woods. Coastal inhabitants harvested reed that was used for roof covering. Floods have always obstructed traditional farming practices in this region. Powerful water washed out the land or covered it with silt, making farming possible only in higher fertile areas protected from floods – this was where farmers growing vegetables and potatoes had settled.

It was obvious that fertile soil was simply meant for grassy vegetation to flourish; therefore floodplain meadows tempted cattle breeders – grassland farmers. Their homesteads or entire villages (Rupkalviai, Pietiniai Girininkai, etc.) were established on elevated areas keeping them away from floods. M. Purvinas (2007) wrote that *“during times of cavalry wars vast grassland areas bore importance similar to modern oil business enterprises”*. They provided livestock with fresh grass and hay, which was supplied to the military and rail horses. Hay was particularly important for goods and passenger traffic, post and household operations. Natural conditions also required adjustment of hay preparation methods. Dried hay used to be stacked on wooden platforms lifted by 0.5–1.0 m above ground to protect it from autumn floods. The harvest was usually removed by sledge in winter, when wet meadows were frozen. Some stacks were transported down the rivers and channels in summer by using large boats. Hay stock was stored in special raised domestic shelters. The rest of it was transported to neighbouring Königsberg and other cities by boats.

Meadows were fully mown, for the forage was of great value in winter. Such meadow-use traditions persisted until the World War II. The war had a significant impact on grassland farmers' lives: polders were abandoned and water pumping stations were destroyed, while some Prussians and farmers

of German descent retired to Germany or were deported to Siberia. Large meadows remained unmanaged or managed poorly, grass was barely harvested and some hay was left rotting in the fields.

A special meadow drainage and management scheme was created in 1953 and installation of new polders began. Two types of polder systems (summer and winter polders) were constructed in the Nemunas Delta. The dikes of the length of 326 km protected the total area of 42 000 ha. The winter polders were employed to protect settlements and cultivated areas from flooding. The summer polders were usually overflowed during the time of spring floods. During the soviet period, the summer polders provided the



Location of polders in the Nemunas Lowland (after Bastienė, Šaulys, 2007)

development of intensive industrial production of grass flour. Establishment of an automated grass forage production depot was initiated in 1959 and 17 production plants were constructed. Grass forage was produced by 12 single-purpose farms, mowing around 10 000 hectares of meadows some 3–4 times per season. Each year, 30 000–40 000 tons of forage was produced.

At the end of the 20th century, a new agricultural reform started. Polder meadows were distributed among smaller owners, leaseholders and enterprises with varied abilities and needs for farming. Due to rising energy prices and decreasing demand for the grass flour forage, its production stopped. Water level adjustment needs also changed, meadows were only used for grass harvesting, use of fertilizers stopped and mowing was performed only once per season (Dainiuvienė, 2001), while other areas were abandoned and remained unmanaged. Changes in farming had a positive impact on biological diversity – number of plants, insects and bird species started to increase. Typical meadow species such as sedge (*Carex* spp.), reed canary-grass (*Phalaris arundinacea*) and meadow foxtail (*Alopecurus pratensis*) returned to cultivated areas, even though less accessible wet meadows remained abandoned and eventually were overgrown with common reed (*Phragmites australis*) and shrubs.





## Culture

For long centuries, the Nemunas Delta region was officially a part of the north-eastern section of German Prussia. Since the 16th century, German writers and historians had called this area “Kleinlittaw” (Lithuania Minor). It is a historical ethnographic region of Prussia, where Lithuanian-speaking population *Lietuvinkai* lived. The area belonged to Prussia until 1945.

Lithuania Minor became very important to Lithuanian culture in the second half of the 19th century. Russian Empire controlled Lithuania at the time. From 1864 to 1904, all publications printed in the Latin alphabet were banned. Most of the Latin-alphabet Lithuanian-language books and periodicals published at



A. Kretchmer. Lithograph „Women of Lithuania Minor dressed in their native costumes“, 19th century

the time were printed in Lithuania Minor (Tilsit, Ragnit, Memel, and Königsberg) and then smuggled into Lithuania by “book carriers” (Lith.: *knygnešiai*). During the final years of the ban, an estimated 30 000 to 40 000 books were smuggled in annually. When caught, the book smugglers were punished by fines, banishment, and exile, including deportation to Siberia. Some were simply shot in the head while crossing the border or executed on the spot.

The first Lithuanian language periodicals appeared during that period in Lithuania Minor, such as *Auszra* edited by Jonas Basanavičius, *Varpas* – by Vincas Kudirka. They had contributed greatly to the Lithuanian national revival of the 19th century.

Nowadays, the Nemunas Delta is impressive structure reflecting the relationship between the population of the region and water, such as Uostadvaris and Ventė lighthouses, the engineering complex of the old water lift station and the old polder engineering equipment. There is a unique architectural ensemble of the Skirvytėlė village. The Mingė village is called Venice of Lithuania, as the River Minija has become its main street. The residues of a unique Žalgiriai (Bismarck) „mire villagers” colony are remaining.

## Biodiversity

More than 600 flowering plant species are found in Nemunas Delta Regional Park and more than 20 of these are listed in the Lithuanian Red Data Book: Spear-leaved skullcap (*Scutellaria hastifolia*), Fringed water-lily (*Nymphoides peltata*), Sand leek (*Allium scorodoprasum*), Early marsh-orchid (*Dactylorhiza incarnata*), Crossleaved heath (*Erica tetralix*), Deer-grass (*Trichophorum cespitosum*), White water-lily (*Nymphaea alba*), etc. Twenty habitat types of Annex 1 of Habitat Directive were identified in the territory. The largest areas are occupied by 3150 Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition* – type vegetation, 6120 Semi-natural dry grassland and scrubland facies on calcareous substrates (*Festuco-Brometalia*), 6270 \*Fennoscandian lowland species-rich dry to mesic grasslands, 6430 Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels, 6450 Northern boreal alluvial meadow, 6510 Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*), 7110 \*Active raised bogs, 7120 Degraded raised bogs still capable of natural regeneration, 9080 \*Fennoscandian deciduous swamp

woods, 9190 Old acidophilous oak woods with *Quercus robur* on sandy plains, 91D0 \*Bog woodlands, 91E0 \*Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alno incanae*, *Salicion albae*)

Vast areas of floodplain meadows as well as raised bogs (Medžioklės, Aukštumala, Berštų, Lietgirių bogs) found in this region are unique in Lithuania. One of these, Aukštumala raised bog is considered *locus classicus* by wetland researchers as it marks the beginning of wetland science worldwide. A monograph by Carl Albert Weber (Weber, 1902), a German botanist who studied vegetation and ecology of Aukštumala raised bog, is the first scientific study on wetland ecosystems in the world.

The Nemunas Delta is the most important bird area in Lithuania. A total of 294 bird species (90% of ornithological fauna of Lithuania) are found in the territory of the Regional Park. Many species are breeding here or use the area as a resting and feeding place during their migration. Several species are considered internationally endangered, e.g. Barnacle goose (*Branta leucopsis*), Common crane (*Grus grus*), Dunlin (*Calidris alpina*) and Aquatic warbler (*Acrocephalus paludicola*). For migratory birds, the Nemunas Delta is one of the most important stop-over areas in the northern part of the Western-Palaeartic migration route. Large numbers of waterbirds congregate at the site on passage (autumn and spring) and during the moulting season, including Tundra swan (*Cygnus columbianus*), Bean goose (*Anser fabalis*), Greater white-fronted goose (*A. albifrons*), Greylag goose (*A. anser*), Tufted duck (*Aythya fuligula*) and Smew (*Mergus albellus*) (BirdLife International, 2017). Annually, 170 bird species are breeding in the Nemunas Delta, and 33 of these are very rare: Aquatic warbler, Corn crake (*Crex crex*), Great snipe (*Gallinago media*), Northern pintail (*Anas acuta*), White-tailed sea-eagle (*Haliaeetus albicilla*), etc.

The Nemunas Delta and the Curonian Lagoon have been long known as the region of fishers. Up to 20 species of fish spawn in polders' canals, Common bream (*Abramis brama*), Northern pike (*Esox lucius*), Crucian carp (*Carassius carassius*) being among the most valued. The polders of the Delta are one of few places in Lithuania, where protected fish Weatherfish (*Misgurnus fossilis*) is found.

Some 50 mammal species are found in the Nemunas Delta, 14 of these are protected species such as Northern birch mouse (*Sicista betulina*), Ermine (*Mustela erminea*), European otter (*Lutra lutra*), and eight bat species



considered rare in Europe, amongst these – Pond and Brandt's bats (*Myotis dasycneme*, *M. brandtii*), Lesser noctule and Common noctule (*Nyctalus leisleri*, *N. noctula*) (Švažas, 2009).





*Gratiola officinalis*



## Excursion sites

### Uostadvaris



### Uostadvaris Water Pumping Station

Uostadvaris is a small village situated 5 kilometres of Rusnė, on the left riverbank of the Atmata River, in the island of Rusnė. There near Dumblys Lake you can find the lowest point in Lithuania – it reaches 0.27 metres below sea level.

In 1907, a water pumping station was built on the Vilkinė River in Uostadvaris. The station had a steam turbine, which absorbed the water excess from grasslands and poured it to the Nemunas River. Even though in 1970, next to the old pumping station, the modern one, driven by electricity, was installed, old Uostadvaris Water Pumping Station is a valuable example of technique, which has become a historical and architectural monument.

Uostadvaris Lighthouse was built on the Atmata River shore in 1873, near to the old water pumping station. It is a square cylindrical red-brick building attached by a passage to the lighthouse keeper's building. Lighthouse is no

longer used for navigation, but now it is the best place to view the panorama of Uostadvaris.

Now there is a lighthouse and a polder museum.

## Uostadvaris alluvial meadows

Hydrological conditions in this summer polder vary within wide range – from long time flooded sites with high water table during growing season to the areas with short flood and moderate conditions. Most wet sites are occupied by *Caricetum gracilis*. The species composition of these communities is different and has been influenced by hydrological changes in the polder over the last decade. Near the lagoon, where the water table is the highest, plant communities are not rich in species and consist of helophytes with admixture of several hygrophytes. More rich in species communities occupy more distant from the lagoon higher places. These *Caricetum gracilis* communities have evolved from *Phalaridetum arundinaceae* over the last decade. They include more hygrophyte species.

*Caricetum distichae* has developed from the part of *Phalaridetum arundinaceae* as well. Such communities include fragments of *Phalaroides arundinacea* stands. Remaining *Phalaridetum arundinaceae* communities are very fragmented and variable depending on hydrological conditions of the site.





*Calthion palustris* communities have developed under moderate conditions. Due to changes in water table, these former mesophyte and hygrophyte communities in lower places include several helophytes as well. In such communities, *Scutellaria hastifolia* occurs. In spite of small area occupied by *Scutellaria hastifolia* in this polder, the age structure of this population is the best compared to other populations in Lithuania.



## Girininkai fluvioglacial dunes



A small stretch of sand dunes reminds of a very interesting and complicated history of the current delta relief formation. The sands of glacial lake, later – estuarine shore sands occur on the surface in many places of the Del-



ta. Sandy plains are more usual, re-drifted low dune streaks are very rare.

Here you can find small fragments of *Koelerio-Corynephoretea* communities. They are not rich in species, but in a relatively small area you can observe different mosaic of open and overgrowing grassland.

### Ragainės vingis floodplain



This is the oldest part of the Nemunas Delta, which is characterized by typical river valley with a broad floodplain. Longitudinal sections of floodplain can be clearly distinguished: riverside, central and pre-mainland.

Different duration of the flood and amount as well as fraction of the deposits, depending on the relief peculiarities, determine the diversity of floodplain vegetation. The lowest sites covered with fine grained silt deposits – peripheral part of the valley and depressions in the central floodplain (former oxbow lakes) – are occupied by tall helophyte communities such as *Caricetum gracilis* and *Phalaridetum arundinaceae*. In the higher places of peripheral part, *Alopecuretum pratensis* communities with inserts of small patches of *Caricetum cespitosae* in the small depressions occur.

Nearly all central part of the floodplain, where the duration of the flood is shorter and alluvium deposits are medium-sized, mesophyte communities prevail. *Arrhenatheretum elatioris* occurs in the large area. These communities vary in species composition depending on hydrological conditions: in the vicinity of the riverbed, they are eumesophytic, while in more distant sites include hygrophilous plants. *Festucetum pratensis* communities occupy small areas, however, are variable as well. More wet places with poorly aerated soils both in central and in peripheral parts of floodplain are occupied by *Deschampsietum cespitosae* communities.

The ridge of sand deposits that stretches along the river bed is occupied by communities with predominant *Petasites spurius* and *Saponaria officinalis*.

In the hygrophyte and mesophyte communities, *Scutellaria hastifolia*, an endangered species in Lithuania and in many European countries, occurs.



*Scutellaria hastifolia*







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