

Grey dune plant communities (*Koelerio-Corynephoretea*) on the Baltic coast in Latvia

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Abstract

The grey dunes along the present-day depositional coasts of Latvia are among the most diverse dune ecosystems in the Baltic Sea region. This paper focuses on the grey dune plant communities, their classification based on the Braun-Blanquet approach and their ecology and distribution in Latvia. A total of 3,430 phytosociological relevés were sampled in all coastal sections in the period from 1994 to 2008. The vegetation was classified using TWINSPAN analysis. Diagnostic species were determined for each syntaxon using statistical measures of fidelity (phi coefficient and Fisher's exact test). The phytogeography of associations and variants is described on the basis of a distribution range analysis of plant species.

In total, three associations of the class *Koelerio-Corynephoretea* occur in the grey dunes. The *Corniculario aculeatae-Corynephorretum canescentis* and the *Caricetum arenariae* belong to the alliance *Corynephorion canescentis* and the order *Corynephorretalia canescentis*. The *Festucetum polesicae* belongs to the alliance *Koelerion glaucae* in the order *Sedo acris-Festucetalia*. With six variants, it is the phytosociologically most diverse association of the grey dunes: typical variant, variant of *Gypsophila paniculata*, variant of *Koeleria glauca*, variant of *Thymus serpyllum*, variant of *Epipactis atrorubens* and variant of *Corynephorus canescens*.

Our results show phytosociological differences among five coastal sections due to geomorphology and coastal processes. The most diverse grey dune plant communities occur on the open Baltic Sea coast where all three associations are represented. The most common vegetation type on all coastal sections in Latvia is the typical variant of the *Festucetum polesicae*. The *Epipactis atrorubens* variant of this association is widely distributed, too. It has its major occurrences along the Gulf of Riga and the Irbe Strait. The *Corniculario aculeatae-Corynephorretum canescentis* was found in only two locations. Stands of the *Festucetum polesicae* var. *Koeleria glauca* occupy wider areas on old dunes, while the *Festucetum polesicae* var. *Gypsophila paniculata* is more typical on young dynamic dunes with intensive sand drift. The results of the phytogeographical analysis of vegetation data show that under the influence of climate, especially with dominance of the oceanic and transformed oceanic air masses, grey dune plant communities on the Latvian coast are mainly sub-oceanic to sub-continental. The most continental community is the *Festucetum polesicae* var. *Koeleria glauca*, while the *Caricetum arenariae* and the *Corniculario aculeatae-Corynephorretum canescentis* have the strongest oceanic character.

Zusammenfassung: Pflanzengesellschaften der Graudünen (*Koelerio-Corynephoretea*) an der Ostseeküste in Lettland

Die naturräumliche Ausstattung Lettlands mit ihren Anlagerungen und Umlagerungen von Sand an den Küsten sowie verschiedenen Klimabedingungen und früheren Landnutzungsformen ist ein Grund dafür, dass die Graudünen von Lettland zu den vielfältigsten Dünenökosystemen der Ostseeküste zählen. In diesem Artikel sind die Forschungsergebnisse über die Pflanzengesellschaften der Graudünen Lettlands zusammengefasst. Im Zeitraum 1994–2008 wurden in typischen Graudünengebieten entlang der Küste von Lettland 3.430 pflanzensoziologische Aufnahmen nach der Braun-Blanquet-Methode erstellt. Die Aufnahmen wurden mit TWINSPAN klassifiziert. Diagnostische Arten der herausgearbeiteten Einheiten wurden anschließend mittels statistischer Treuemaße (phi-Koeffizient, Fishers exakter Test) ermittelt. Die phytogeographische Analyse der Assoziationen und Varianten wurde auf Grundlage der Artenzusammensetzung der Vegetation vorgenommen.

Insgesamt kommen drei Assoziationen aus der Klasse *Koelerio-Corynephoretea* in den Graudünen vor. Das *Corniculario aculeatae-Corynephorretum canescentis* und das *Caricetum arenariae* gehören zum Verband *Corynephorion canescentis* in der Ordnung *Corynephorretalia canescentis*. Das *Festucetum polesicae* wird zum Verband *Koelerion glaucae* in der Ordnung *Sedo acris-Festucetalia* gestellt. Mit 6 Varianten (Typische Variante, *Gypsophila paniculata*-Var., *Koeleria glauca*-Var., *Thymus serpyllum*-Var., *Epipactis atrorubens*-Var. und *Corynephorus canescens*-Var.) ist es die vielfältigste Assoziation der Graudünen. Der Vergleich von fünf geomorphologisch und landschaftlich unterschiedlichen Küstenabschnitten zeigt,

dass die Vielfältigkeit der Graudünengesellschaften an der offenen Ostseeküste mit Vorkommen aller drei Assoziationen am höchsten ist.

Die häufigste Pflanzengesellschaft an der ganzen Ostseeküste ist die Typische Variante des *Festucetum polesicae*. Weit verbreitet ist auch die *Epipactis atrorubens*-Variante des *Festucetum polesicae*, die an der Ostseeküste des Meerbusens und der Meeresecke von Irbe festgestellt wurde. Die Verbreitung des *Corniculario aculeatae-Corynephorretum canescentis*, das nur an zwei Orten vorkommt, ist durch einen Mangel an Störungen eingeschränkt. Das *Festucetum polesicae* in der Variante von *Koeleria glauca* ist in den älteren Graudünen am häufigsten, während die Variante von *Gypsophila paniculata* vor allem in Bereichen mit stärkeren Sandverwehungen auftritt. Die Ergebnisse der phytogeographischen Analyse zeigen, dass die Graudünengesellschaften in Lettland vorwiegend subozeanisch bis subkontinental geprägt sind. Das *Festucetum polesicae* in der Variante von *Koeleria glauca* ist besonders kontinental, das *Caricetum arenariae* und das *Corniculario aculeatae-Corynephorretum canescentis* sind dagegen am stärksten ozeanisch geprägt.

Keywords: dune vegetation, *Festucetum polesicae*, nature conservation, sandy dry grassland, syntaxonomy, succession stage, synchronology.

1. Introduction

Coastal grey dunes are relatively stable in terms of succession and are colonised by a more or less closed vegetation of herbaceous vascular plants, lichens and mosses in places where soil has begun to develop. Grey dunes are generally located between the young white dunes near the beach and the older brown dunes covered by heathlands and woodlands of later succession (WIEDEMANN & PICKART 2004, HOUSTON 2008). In landscape-ecological terms, grey dunes belong to the dry component of the 'stressed dune landscape' where biological dynamics are in equilibrium between 'top down' regulating stress factors and 'bottom up' community succession (DOODY 1994, PROVOOST et al. 2004). The grass communities of Baltic grey dunes mainly belong to the class *Koelerio-Corynephoretea*. Due to differences of coastal types and geological processes there is a high diversity of grey dune plant communities in the Baltic Sea region (HUNDT 1985, PIOTROWSKA 1988, KOEHLER & WEIDEMANN 1992, HALLEMAA 1999, STANKEVIČIŪTE 2000, CHRISTENSEN & JOHNSEN 2001a, DENGLER 2004).

In the EU Habitats Directive (92/43/EEC), fixed coastal dunes with herbaceous vegetation (grey dunes, habitat type 2130) are included as a priority habitat type requiring special protection (EUROPEAN COMMISSION 2007). This means that it is necessary to ensure a favourable conservation status (in terms of quality and range) for this habitat type within each biogeographical region. This is possible only with effective management measures based on knowledge of the ecology and distribution of plant communities.

From the phytogeographical perspective, the territory of Latvia belongs to the Baltic province, which is divided into western and eastern Baltic subprovinces (LAASIMER et al. 1993). The first scientific phytogeographical divisions of the Baltic carried out by KUPFFER (1911), WAHL & KUPFFER (1911), WEGNER (1911) and KUPFFER (1925) described features of the coasts of Estonia, Latvia and Lithuania. According to these authors, the seashore of Courland and Livonia is characterised by psammophytic vegetation of the Baltic province. This psammophytic vegetation of coastal dunes was dominated by *Festuca sabulosa* (= *F. polesica*), *Koeleria glauca*, *Carex arenaria*, *Thymus serpyllum*, *Dianthus arenarius*, to a lesser extent also by *Corynephorus canescens*, as well as bryophyte and lichen communities (KUPFFER 1912, 1925, 1927). Studies in the Riga region have described the rich diversity of the coastal shifting dunes (STOLL 1931). Some species like *Petasites spurius*, *Epipactis atrorubens*, *Astragalus arenarius*, *Tragopogon heterospermus* and *Dianthus arenarius* were common. *Arabidopsis arenosa*, *Alyssum gmelinii*, *Pulsatilla pratensis* were recorded as spring-aspect plants. The larger diversity and more dynamic forms of dune plant communities described at that time were more characteristic for the eastern Baltic region than for the territory of the Kaliningrad Oblast (GESINSKI 1932). Plant communities referred to as *Festucetum*, *Equisetetum*, *Caricetum*, *Koelerietum*, *Thymetum lichenosum* and *muscosum*, *Pinetum*, *Betuletum* and *Salicetum* were present in the vegetation of the Gulf of Riga coast. Vegetation successions on the Livonia coast described in the 1930s varied among coastal zones, mainly depending on wind strength, sand type, temperature and precipitation (GESINSKI 1932).

A new period in phytosociological investigations of the Latvian seacoast started with the publishing of an overview of vascular plant species composition and vegetation of the Coastal Lowland geobotanical district in 1974 (TABAKA 1974). The vascular plant species list (1,212 species) was based on a large database of herbaria, literature and geobotanical descriptions (BIRKMANE & JUKNA 1974, TABAKA 1974). The phytogeographical analysis has shown that the majority of these plant species has a boreo-temperate and submeridional distribution, while only a small number of species represent temperate European species. The Latvian coast is a transitional zone where East European plant species (e.g. *Astragalus arenarius*, *Dianthus arenarius*, *Alyssum gmelinii*) and Atlantic European species (e.g. *Carex arenaria*, *Cakile maritima*, *Corynephorus canescens*, *Juncus balticus*, *Leymus arenarius*) are growing side by side (FATARE 1974a, KĻAVIŅA 1974a, 1974b). Based on the distribution areas of native vascular plant species in the territory of Latvia (in total 1,123 taxa), FATARE (1992) recognised a littoral plant species group with 51 species.

The studies of the Coastal Lowland geobotanical district in the 1970s included dune vegetation of 32 sites along the coast, but data on grey dune plant communities were not summarised in vegetation tables, and only typical plant species were recorded (FATARE 1974b). Investigations of dune vegetation using the Braun-Blanquet approach started after Latvia regained its independence in 1991 when restrictions to visit the seashore were abolished. Most of the collected phytosociological data of the *Koelerio-Corynephoretea* communities are summarised in a dune habitat monitoring database (years 2001–2007) managed by the Faculty of Biology, University of Latvia, as well as presented in several reviews and papers (OFKANTE 1997, 1999, LAIME 2001, ROVE 2001, LAIME 2002, RUDŽĪTE 2004, PĪTERĀNS et al. 2005, RUDŽĪTE 2006, KABANOVA 2008).

The main goal of the present paper is to provide a brief survey of classification, ecology and distribution of Latvian grey dune plant communities.

2. Study area

2.1. Coastal types

Data were collected in the grey dune area on the Baltic Sea coast of Latvia (Fig. 1). The main coastal zones developed from the Litorina Sea transgression and the subsequent regression 7,000–2,800 years ago (ULSTS 1998). For example, the grey dune area in the town Pāvilsta is located on the Litorina Sea terrace (LAIME et al. 2006), and dune grasslands in the village Pape are located within the depositional neck of the Litorina Sea (LAIME et al. 2007). According to the morphogenetic classification of the Baltic Sea coasts, the eastern part of Latvia and Lithuania mainly belongs to straightened depositional coasts (GUDELIS 1967), which are rich in primary and semi-fixed dunes. The seashore in Latvia extends over 497 km in length, 254 km along the open Baltic Sea and 243 km along the Gulf of Riga, respectively. Based on geological structure, composition of the substrate and coastal geological processes during the past 30–50 years, two groups of coastal types can be distinguished in Latvia: cliffs and depositional coasts (EBERHARDS 2003). ULSTS (1998) additionally recognises dynamic equilibrium coasts.

The Baltic Sea coast in Latvia is on average 4 m above sea level, but in some places it reaches 15 m or more. Aeolian activity on beach and primary dunes is one of the most important ecological factors affecting vegetation structure and species composition of grey dunes. In Latvia, there is a large variation in spatial features of aeolian processes, depending on coastal orientation, topography, beach width, foredune height, slope, topography as well as human influence (EBERHARDS 2006). Beaches are mostly sandy (approximately 240 km or 45% of the total coast line), and the width of beaches varies between 8 and 200 m. Sand-gravel and pebble beaches stretch over 154–180 km of the coast. About 70 km of the seashore consists of narrow zones of bare gravel, pebble and boulder, in places overgrown with reeds and rushes (EBERHARDS 2006).

Characteristic plant species of dry beaches are *Salsola kali*, *Cakile baltica* and *Atriplex littoralis*. The typical coastal topography of Latvia includes primary dunes (embryonic dunes and white dunes), which have a total coastline length of approximately 226 km in Latvia. There are

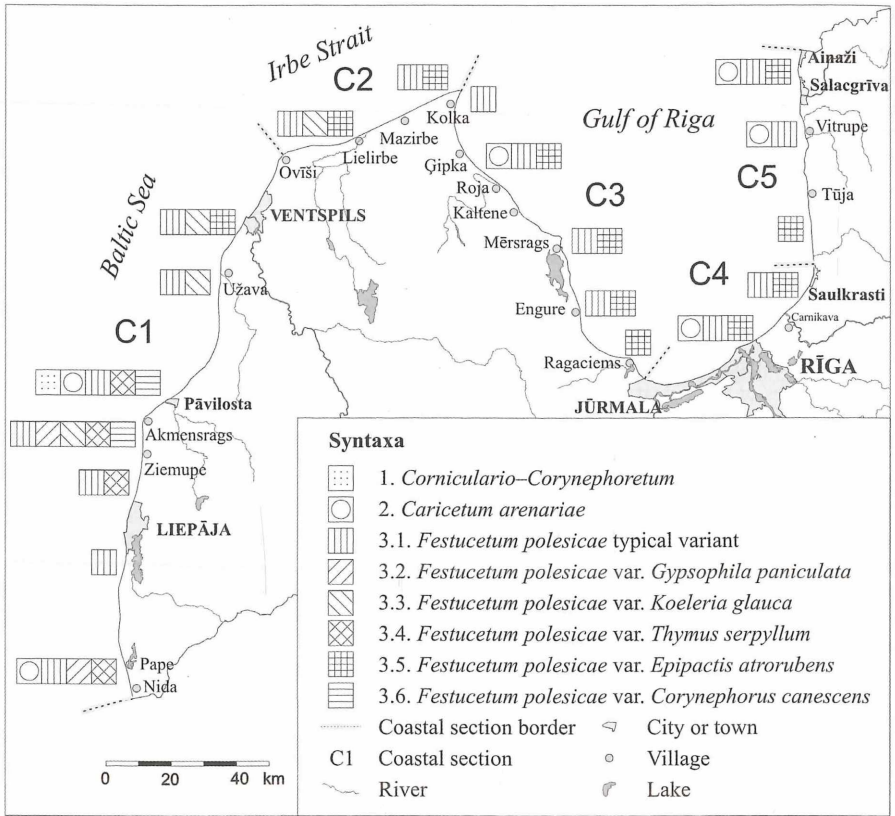


Fig. 1: Distribution of grey dune communities along the Baltic Sea coast in Latvia. Coastal sections are: C1: Nida-Cape Ovišrags Coast, C2: Irbe Strait Coast, C3: Kurzeme Coast, C4: South Coast and C5: Vidzeme Coast (after EBERHARDS 2003).

Abb. 1: Verbreitung der Pflanzengesellschaften der Graudünen an der Ostseeküste in Lettland. Für die Bezeichnung der einzelnen Küstengebiete siehe englische Abbildungsunterschrift.

areas with two or three parallel white dunes about 1.5 to 2.5 m in height, but others can reach 5 to 10 m in height. White dunes are dominated by *Ammophila arenaria*, accompanied by *Anthyllis maritima*, *Leymus arenarius*, *Festuca arenaria* and *Hieracium umbellatum* (EBERHARDS 2006). The greater part of grey dunes is associated with white dunes, although there are some large grey dune territories close to the erosion coast. The width of the grey dunes varies from 5–20 m in narrower open dune belts to 100–500 m on the widest open coasts (LAIME & ROVE 2001). Dune grassland habitats are more distributed around towns, villages and roads where sand drifting has been promoted by human activities such as deforestation, burning and grazing by livestock during the last centuries (BUŠS 1960, EBERHARDS 2006).

At the beginning of the 19th century, when moving dunes in Latvia reached an area of approximately 8,000 ha, dune afforestation was initiated along the entire coast (ZVIEDRIS 1949). Already in 1838, a special instruction for a 320 m wide coastal zone was issued, and mobile dune stabilisation projects lasted more than 130 years. The open secondary dune landscape has remained mainly around settlements (e.g. Pape, Akmenšrags, Pāvilosta, Rīga). Between 1940 and 1990, the traditional economical and cultural environment in many locations along the coastal zone was degraded because of military activities of the Soviet Union. While dune management by grazing or mowing was stopped in some areas, new disturbances within firing ranges, rocket bases and other military territories promoted grey dune vegetation and limited overgrowth of pine.

Under the influence of wind and waves, littoral drift moves to the north along the open Baltic Sea from Nida to Cape Kolkastrags and from northwest to southeast along the west coast of the Gulf of Riga (ULSTS 1998). In relation to these drift flows and other coastal processes and to the dominant habitats and vegetation, the Latvian seacoast can be divided into five sections: the Nida-Cape Ovištrags Coast (C1), the Irbe Strait Coast (C2), the Kurzeme Coast (C3), the South Coast (C4) and the Vidzeme Coast (C5) (EBERHARDS 2003; see Fig. 1). The largest grey dune areas are located on the open Baltic coast and the South Coast (sections C1, C2 and C4). Habitat mapping showed that grey dunes occupy a total area of approximately 1,510 ha in Latvia (ZNOTIŅA et al. 2006).

2.2. Climate

Latvia is located in the temperate zone between the oceanic and the interior regions of Europe. The mean annual air temperature is +5.8 °C with a range of 2.2 °C and reaches the highest value (6–7 °C) in Riga and on the open Baltic coast. The average temperature has increased by 1.4 °C during the last 155 years (LIZUMA et al. 2007). On the Latvian coast, the mean temperature ranges from –4.5 °C in January to +16.8 °C in July. The lowest temperatures on the seacoast usually occur in February (from –18 °C to –24 °C). Winters are slightly colder on the east coast (sections C4 and C5 in Fig. 1) than on the west coast (BRIEDE 2005).

Oceanic and transformed oceanic air masses (85% of all air masses) dominate along the coast throughout the year while the mean frequency of continental air masses is only 15% (DRAVENIECE 2007). Annual precipitation is 630–650 mm on the east coast and from 601 mm on the northwest coast (the Cape Kolkastrags) to 686 mm on the southwest coast (BRIEDE & LIZUMA 2007). The monthly precipitation minimum is usually in February and March (mean 26–39 mm), and maximum in July and August (BRIEDE 2005). One of the most significant ecological factors is a persistence of snow cover, which can directly influence soil humidity and length of growing season. During 1945–2004, there were on average 70 days per year with snow cover on the west seacoast and 95 days on the east seacoast (DRAVENIECE et al. 2007). The mean seasonal depth of the snow is a few centimetres, with a maximum of 15–25 cm.

Severe disturbances to the dune area and the vegetation result from southwest and west gale winds. Storms occur more frequently in autumn and winter. In 2005, hurricane Erwin, the second strongest storm during the last one hundred years, damaged 40% of the seashore of Latvia. The total volume of material washed out from the coastal zone was over three million cubic metres of sediment (EBERHARDS et al. 2006). A deficit of sand was observed in many coastal areas after this impact.

3. Material and methods

3.1. Main principles of syntaxonomical treatment

For the phytosociological description and classification, we used the Braun-Blanquet approach modified to remove some of the earlier subjective aspects. The following principles were followed:

- The transect approach is advisable to describe the coastal dune vegetation. The main purpose in using transects in grey dunes is to include the existing variation in plant cover (KENT & COKER 1996).
- Sample plots of the complete vegetation, including ecotones, are taken into account for classification (DENGLER et al. 2006).
- The diagnostic species combination contains differential species and character species. Both of them must fulfil the differential species criterion: the percentage constancy of a species in a syntaxon must be at least twice as high as that in another syntaxon of the same rank. Additionally for differential species: the percent constancy of species in the differentiated syntaxon must be at least 10% higher than in the compared syntaxon/a where it must not exceed 20%. Character species of a syntaxon must fulfil the differential species criterion compared with all other syntaxa of the same rank within the same structural type (DENGLER 2003, DENGLER et al. 2005).
- Within each syntaxon of superior rank, one central syntaxon of the next lower rank can be distinguished and characterised by diagnostic species of the syntaxonomic level(s) above, but has insufficient or no character species of its own (DENGLER et al. 2005, DENGLER et al. 2006).

– Fidelity expresses the diagnostic value of the species for a particular syntaxon: species with a phi coefficient above 0.25 are diagnostic, while species with a phi coefficient above 0.50 are highly diagnostic (CHYTRÝ 2007).

– For sufficient characterisation of syntaxa, constant and dominant species should be taken into account. Constant species are species frequently occurring in the vegetation unit (constant species with a frequency over 40%, highly constant species with a frequency over 80%) and species with high cover (dominant and highly dominant species with a cover value of 25% in at least 5% or 10% of relevés, respectively (CHYTRÝ 2007).

3.2. Vegetation data collection

Vegetation data were collected between 1994 and 2008 in typical grey dune areas of all coastal sections (Fig. 1). The research included only grey dunes located close to the seashore and more or less under direct influence of coastal geological processes. For most of the sample plots, a wooden frame (1 m × 1 m) was placed along transects oriented perpendicular to the coastline. Transects were located between primary dunes, a cliff or a beach on the seashore and woodland, farmland or built-up territory in the inland direction. Plots were interspersed by distances of 1–3 m, depending on the width of the grey dune belt and plant cover homogeneity. Deviating from the majority, 228 sample plots were 2 m × 1 m in size and sometimes orientated parallel to the coastline.

The vegetation description was carried out according to the Braun-Blanquet method (BRAUN-BLANQUET 1964). A five-degree scale of cover was used: + (less than 1% cover); 1 (1–5%); 2 (6–25%); 3 (26–50%); 4 (51–75%); 5 (76–100%). A total of 3,430 phytosociological relevés were sampled and stored in a Visual FoxPro Database management system. Plot coordinates were determined with a Global Positioning System (GPS; see Appendix A).

3.3. Nomenclature

In general, the names of taxa follow GAVRILOVA & ŠULCS (1999) for vascular plants, ĀBOLIŅA (2001) for bryophytes and PITERĀNS (2001) for lichens. In delimitating and naming the phytosociological classes, we follow the European overview by MUCINA (1997). Plant community nomenclature follows the International Code of Phytosociological Nomenclature (WEBER et al. 2000; see DENGLER 2004).

3.4. Vegetation data analysis

Relevés were analysed with the program JUICE (TICHÝ & HOLT 2006) and classified by two-way indicator species analysis (TWINSPAN, HILL 1979). The following settings were applied: pseudospecies cut levels 5, values of cut levels 0, 1, 5, 2, 50; maximum level of division 6. The hierarchical syntaxonomical level of the individual TWINSPAN clusters was determined based on the plant species composition of each cluster, literature data and the ecology of the described grey dune vegetation.

In the phytosociological classification we followed the principles given in section 3.1. Diagnostic species for each syntaxon were determined using species constancy, cover and fidelity. The phi coefficients were applied to the data set with relevé groups of equalised size and were calculated only within the next superior syntaxon (CHYTRÝ et al. 2002, TICHÝ & CHYTRÝ 2006). In the synoptic table, the phi coefficient is only shown if it is positive and significant according to Fisher's exact test at $\alpha = 0.001$. This probability level was used because in large phytosociological data sets Fisher's exact test may yield very small probability values and for practical reasons $\alpha = 0.001$ was more useful than lower significance levels.

The continentality value of species is based on ROTHMALER (1976), ELLENBERG et al. (1992), and OBERDORFER (2001). For some vascular plant species not included in the mentioned sources, distribution maps (HULTÉN & FRIES 1986) were used additionally to evaluate their continentality. Seven continentality groups were distinguished: continental and weakly continental; subcontinental; weakly sub-oceanic and weakly subcontinental; suboceanic; oceanic and weakly oceanic; indifferent; and not classified. The continentality values of each syntaxon were obtained by calculating the mean number of species and the mean total cover of species in each continentality group, respectively. The mean values were calculated based on the individual relevé values.

3.5. Soil sampling and analysis

In 2006 and 2007, soil samples were taken in 10 grey dune sites in the framework of the project "Monitoring of coastal habitats". Soil samples of the upper layer (depth 10 cm) were taken at several points of a phytocoenosis in autumn. The soil samples were chemically analysed in the soil laboratory of

the Faculty of Biology, University of Latvia. Before the analysis, the samples were dried at 80 °C and then sieved through a 2 mm mesh. For each sample, pH (H₂O) was determined in a suspension of 5 g fine soil in 20 ml H₂O after shaking (1 hr) and standing (16 hrs), and pH (KCl) in a suspension of 5 g fine soil in 20 ml KCl solution after shaking (1 hr) and filtration. The concentration of Ca²⁺ was determined in concentrated HNO₃ extracts, following the MANUAL FOR INTEGRATED MONITORING (1998) with an atomic absorption spectrometer (Varian Techtron 1100). Total N was determined by the Kjeldahl method (KJELDAHL 1883).

4. Results

4.1. Phytosociological characterisation

The described grey dune vegetation of Latvia can be classified into two orders, two alliances and three associations one of which is further subdivided in six variants:

Class: *Koelerio-Corynephoretea* Klika in Klika & V. Novák 1941

Order: *Corynephorotalia canescentis* Klika 1934

All.: *Corynephorion canescentis* Klika 1931

Assoc. 1: *Corniculario aculeatae-Corynephorum canescentis* Steffen 1931 nom. invers. propos.

Assoc. 2: *Caricetum arenariae* Christiansen 1927

Order: *Sedo acris-Festucetalia* Tx. 1951 nom. invers. propos.

All.: *Koelerion glaucae* Volk 1931

Assoc. 3: *Festucetum polesicae* Regel 1928

Var. 3.1: typical variant

Var. 3.2: variant of *Gypsophila paniculata*

Var. 3.3: variant of *Koeleria glauca*

Var. 3.4: variant of *Thymus serpyllum*

Var. 3.5: variant of *Epipactis atrorubens*

Var. 3.6: variant of *Corynephorus canescens*

In the synoptic table (Table 1), species constancy values and fidelities for each community are presented. Each syntaxon is characterised by a relevé table (Tables 2 and 3 in the Supplement) with complete species list and cover values presented, based on 35 randomly chosen relevés per syntaxa. Information for relevé sampling locations (latitude, longitude and plot size) is given in Table 4. Soil data for 10 locations are included in Table 4. Fig. 1 shows the distribution of the main localities of plant communities. Fig. 2 shows the communities' degree of continentality.

4.2. Characterisation of the associations and variants

4.2.1. *Corniculario aculeatae-Corynephorum canescentis*

This community represents early succession stages of grey dune vegetation (Fig. 3). The grass *Corynephorus canescens* is the main differential species that separates the *Corniculario-Corynephorum* from the other communities investigated (Table 1 and Table 2 in the Supplement). The initial stage of the *Corniculario-Corynephorum* contains very few moss and lichen species (mean cover 5–20%), in some cases only *Polytrichum juniperinum*, in others also *Cetraria aculeata* and *C. muricata*. Among vascular plants, *Corynephorus canescens* dominates (mean cover 10%); other species, e.g. *Carex arenaria*, *Festuca sabulosa* and *Hieracium umbellatum*, are scattered with 1–5% cover. In the next succession stage, there is a greater total cover of bryophytes and lichens (50–60%), where *Polytrichum juniperinum* covers on average 50%, *Cetraria* species 1–5% and *Cladina mitis* 15%. A part of the relevés within the *Corniculario-Corynephorum* represents a lichen-rich grey dune vegetation, which is a contact community to the *Festucetum polesicae* var. *Corynephorus canescens*.

On the Baltic Sea coast in Latvia, the *Corniculario-Corynephorum* is rare, and *Corynephorus canescens* is on the northern edge of its distribution area (ĀNDRUŠAITIS 2003). Most of the described relevés originated from the town of Pāvilosta, which is the main distribution area of this association on the Latvian coast. Historically, these open dunes (former white dunes) were used for drying of fishing nets and also algae, and were formerly grazed and occasionally

Table 1: Abridged synoptic table of grey dune communities in Latvia.

The first figure in the columns indicates percentage constancy values, while the second, superscript figure is the phi coefficient $\times 100$. Phi coefficients are only shown if a species showed a non-random accumulation within a certain column as assessed with Fisher's exact test at $\alpha = 0.001$. Character species are indicated by dark shading, differential species of variants by light shading, differential and other species of variants of diagnostic value by frames. Other taxa are arranged in order of occurrence. Species occurring in less than 10 relevés are shown at the end of the table.

Column headers: Assoc. 1. – *Corniculario aculeatae-Corynephorum canescens*, Assoc. 2. – *Caricetum arenariae*, Assoc. 3. – *Festucetum polesicae*, Var. 3.1. – typical variant, Var. 3.2. – variant of *Gypsophila paniculata*, Var. 3.3. – variant of *Koeleria glauca*, Var. 3.4. – variant of *Thymus serpyllum*, Var. 3.5. – variant of *Epipactis atrorubens*, Var. 3.6. – variant of *Corynephorus canescens*.

Tab. 1: Gekürzte Stetigkeitstabelle der Pflanzengesellschaften der Graudünen Lettlands.

Der erste Wert innerhalb einer Spalte gibt die prozentuale Stetigkeit, der zweite Wert den phi-Koeffizient $\times 100$ an (nur signifikante phi-Koeffizienten sind dargestellt; Fisher-Test, $\alpha = 0,001$). Charakterarten sind dunkelgrau und Differenzialarten hellgrau hinterlegt, Differenzialarten zusammen mit anderen charakteristischen Arten durch Rahmen gekennzeichnet. Arten, die in weniger als 10 Aufnahmen vorkam, sind in der Fußnote aufgelistet. Für die Überschriften der Spalten siehe englische Tabellenüberschrift.

	Assoc. 1.	Assoc. 2	Assoc. 3	Var. 3.1.	Var. 3.2.	Var. 3.3.	Var. 3.4.	Var. 3.5.	Var. 3.6.
Number of relevés	45	148	3237	652	359	790	525	675	236
Mean number of plant taxa (total)	6.2	6.4	10.2	7.7	9.2	7.0	10.4	16.3	11.7
Mean number of vascular plants	1.9	5.1	6.7	5.5	5.0	5.2	6.4	11.7	4.3
Mean number of bryophytes	0.9	1.2	1.7	1.5	2.3	1.0	2.3	1.9	1.5
Mean number of lichens	3.4	0.1	1.8	0.8	1.9	0.8	1.6	2.6	5.9
Mean cover of plants (%)	65	53	63	49	54	36	71	97	86
Mean cover of vascular plants (%)	19	40	36	34	34	22	37	58	31
Mean cover of bryophytes (%)	22	13	16	12	13	12	27	18	16
Mean cover of lichens (%)	24	1	11	4	7	3	7	21	39
Mean plot size (m ²)	1.00	1.00	1.00	1.02	1.00	1.00	1.00	1.31	1.00
Class Koelerio-Coryneporetea									
<i>Festuca sabulosa</i>	76	10	88 ⁴³	86	92	94 ⁸	95 ⁹	76	88
<i>Hieracium umbellatum</i>	4	39	62 ³⁹	56	24	58	68 ⁹	89 ²⁸	54
<i>Carex arenaria</i>	9	97 ⁶⁴	48	55 ²	24	12	85 ²⁹	54 ²	85 ²⁹
<i>Sedum acre</i>		39	39	37	76 ³³	11	62 ²⁰	51 ¹⁰	4
<i>Brachythecium albicans</i>		46 ³⁴	29	31	45 ¹⁶	5	39 ¹⁰	48 ¹⁹	7
<i>Artemisia campestris</i>		27	34 ²⁴	42 ¹¹	36	16	21	67 ³⁵	2
Association Corniculario aculeatae-Corynephorum canescens									
<i>Corynephorus canescens</i>	98 ⁹⁵		5	1	1		7	1	48 ⁵⁹
<i>Petroria aculeata</i>	64 ⁶⁰		16	7	12	7	37 ²⁰	15	39 ²²
<i>Polytrichum juniperinum</i>	58 ⁶⁷		2	1		1	1	6 ⁹	8 ¹⁴
<i>Cladina mitis</i>	49 ⁵³		9	1			2	15	77 ⁷⁵
<i>Pycnothelia papillaria</i>	42 ⁵⁷		1						3 ¹⁵
<i>Cladonia floerkeana</i>	40 ⁵⁰		5	1		1	1	3	54 ⁶⁷
<i>Cladonia pyxidata</i>	38 ⁵¹		2	2	1	3		2	6 ¹¹
<i>Cladonia gracilis</i>	33 ³⁹	1	8	1	5	1	6	13	53 ⁵⁴
<i>Cetraria muricata</i>	22 ³⁹		1				1	1	2
<i>Cladonia verticillata</i>	22 ³⁵		3	1				14 ²⁷	6
Association Festucetum polesicae									
<i>Tortula ruralis</i> agg.		21	45 ³⁹	43	75 ²⁹	39	45	52 ⁹	4
<i>Koeleria glauca</i>			41 ⁵⁶	18	4	86 ⁴⁶	23	42	46
<i>Ceratodon purpureus</i>		6	29 ³⁸	28	67 ³⁶	32	35	9	10
<i>Dianthus arenarius</i>			12 ²⁹	2		17 ⁸	15	19 ¹²	14
Festucetum polesicae var. Gypsophila paniculata									
<i>Gypsophila paniculata</i>		26 ³²	8	2	68 ⁷⁸	1	1	1	
<i>Cladonia fimbriata</i>			13 ³¹	3	45 ³⁶	1	20 ⁶	20 ⁵	5
<i>Cladonia coniocraea</i>		1	5	1	35 ⁵¹			2	2
<i>Erophila verna</i>			3		26 ⁴⁷	1		1	
<i>Cerastium semidecandrum</i>		1	3	1	23 ⁴³		1	1	
<i>Silene borysthena</i>			2	2	16 ³³	1		1	

Assoc. 1. Assoc. 2 Assoc. 3 Var. 3.1. Var. 3.2. Var. 3.3. Var. 3.4. Var. 3.5. Var. 3.6.

Festucetum polesicae var. Koeleria glauca

<i>Pulsatilla pratensis</i>		12 ²⁹	1			34 ⁴⁰	1	16 ¹²	1
<i>Astragalus arenarius</i>		5 ¹⁸	2			17 ³⁴	1		
<i>Alyssum gmelinii</i>		5 ¹⁹	1	1		17 ³²		3	
<i>Diploschistes muscorum</i>		2				8 ²⁶			
<i>Lecanora muralis</i>		2				7 ²⁵			

Festucetum polesicae var. Thymus serpyllum

<i>Hypnum cupressiforme</i>	5	9	5	9	1	42 ⁴⁶			8	
<i>Pohlia nutans</i>		4 ¹⁶	1	6	1	17 ²⁸		1		
<i>Viola tricolor</i>	1	5	4	5	1	15 ²²		3	1	
<i>Thymus serpyllum</i>	2	1	33 ⁴⁶	9	8	41 ⁹		85 ⁵⁰	22	29
<i>Galium mollugo</i>		47 ³³	32	46 ¹⁶	13	16		60 ³⁰	37	6

Festucetum polesicae var. Epipactis atrorubens

<i>Honckenya peploides</i>	1	14 ³⁰	7	1	1		1	61 ⁶⁹		1
<i>Epipactis atrorubens</i>		14 ³¹	3	1	9			54 ⁶²		
<i>Festuca arenaria</i>	17	13	15	12	7	1		31 ²⁹		
<i>Peltigera canina</i>		5 ¹⁸	1					22 ⁴⁰		2
<i>Jasione montana</i>		4 ¹⁶	1				2	14 ²³		7
<i>Cardaminopsis arenosa</i>		4 ¹⁷	2		3	1		14 ²⁸		
<i>Silene nutans</i>	1	3	2		1	1		12 ²⁷		1
<i>Viola canina</i>		1	2	1		1		11 ³⁰		
<i>Racomitrium canescens</i>	31	16 ¹	4	1	10	10		47 ³⁸		25 ¹¹
<i>Anthyllis maritima</i>	1	15 ³⁰	4		25 ¹⁸	1		40 ⁴⁰		

Festucetum polesicae var. Corynephorus canescens

<i>Polytrichum piliferum</i>	2	1	5	1	2	1	1	53 ⁶⁷		
<i>Cladonia glauca</i>			8 ²⁴	9	1	1	1	48 ⁵⁰		
<i>Cladonia phylophora</i>	7		6	1	1	1		14 ⁶		42 ⁴⁹
<i>Cladonia cornuta</i>	7		9 ¹¹	3	9	1	9	12		38 ³⁶
<i>Cetraria islandica</i>	4	1	4	2	1	1	3	35 ⁵¹		
<i>Cladonia coccifera</i>			2	2		1		26 ⁴⁵		
<i>Dicranum fuscescens</i>	2	1	1	1		1		13 ³⁰		
<i>Cladonia furcata</i>	3	6	6	1	1	5	10 ⁶	19 ²²		

Class Ammophiletea

<i>Calamagrostis epigeios</i>	2	11	22 ²³	40 ²⁰	18	4	20	36 ¹⁶	10
<i>Leymus arenarius</i>		14	20 ²⁰	29 ¹⁴	13	2	4	55 ⁴⁵	1
<i>Ammophila arenaria</i>		1	19 ³⁶	17	6	17	5	48 ⁴⁰	1
<i>Tragopogon heterospermus</i>		1	10 ²⁵	11	14	9	7	15 ⁹	
<i>Lathyrus maritimus</i>		1	3	7 ⁸	13 ²¹	1	1	1	
× <i>Calammophila baltica</i>			2	8 ¹⁹	1	1	2	1	

Other taxa

<i>Pinus sylvestris</i>		1	17 ³³	1		3	1	72 ⁷⁵	8
<i>Salix daphnoides</i>			11 ²⁸	2	1			52 ⁶⁷	
<i>Cladonia chlorophaea</i>	2	1	10 ²⁰	10	1	7	1	23 ¹⁹	18 ¹²
<i>Cetraria ericetorum</i>	7		10 ¹⁴	1	39 ²⁸		15	2	39 ²⁸
<i>Hypogymnia physodes</i>			7 ²²	2	22 ²³	5	11 ⁶	4	3
<i>Pleurozium schreberi</i>	7	5	4	1	1	7		12 ¹⁵	6
<i>Dicranum scoparium</i>	1	4	1	1			10 ¹²	8 ⁸	6
<i>Peltigera rufescens</i>		4 ¹⁷	6		3		9 ¹¹	5	2
<i>Racomitrium ericoides</i>		4 ¹⁷	5	13 ¹⁷	3	6			2
<i>Cladonia scabriuscula</i>		1	3	6 ⁶	1	1	1	7 ⁹	6
<i>Achillea millefolium</i>		29 ⁴³	2	2			5 ⁹	6 ¹²	
<i>Calluna vulgaris</i>		1	2	1	1	2		7 ¹³	5
<i>Arctostaphylos uva-ursi</i>			4			7 ¹³	1	9 ¹⁷	
<i>Cladonia deformis</i>			3				1	13 ²⁵	6
<i>Cladonia subulata</i>			3	1	1	3		9 ²⁰	1
<i>Thuidium abietinum</i>	3	3	7 ¹²				6 ⁸	3	1
<i>Peltigera didactyla</i>	1	3	6 ¹¹	1			6 ¹¹	3	
<i>Galium boreale</i>	1	3	1		2		1	10 ²⁴	
<i>Cladina arbuscula</i>		3	1	12 ²³			2	5 ⁴	
<i>Linaria vulgaris</i>	14 ²⁷	2	1	1			2	5 ¹⁴	
<i>Cladina rangiferina</i>		3	1	1	1		9 ¹⁴	1	10 ¹⁶
<i>Hieracium pilosella</i>	2	2	1	1	1		6 ¹⁰	4 ⁶	3

Assoc. 1. Assoc. 2 Assoc. 3 Var. 3.1. Var. 3.2. Var. 3.3. Var. 3.4. Var. 3.5. Var. 3.6.

<i>Cladonia squamosa</i>	4		2	1		1	1	9 ²¹	4
<i>Taraxacum officinale</i>		8 ¹⁹	2	3	1	1	6 ¹⁴	1	1
<i>Salix rosmarinifolia</i>		1	2	1		8 ²²		1	
<i>Empetrum nigrum</i>			2	1		1	1	8 ²²	1
<i>Cladonia rangiformis</i>			2	1	1	1	6 ¹⁴	4 ⁷	
<i>Solidago virgaurea</i>			2	1		1	1	8 ²⁴	
<i>Ditrichum flexicaule</i>			2	1	3	4 ⁶	3		
<i>Cladonia</i> sp.			2			6 ¹⁶	1		2
<i>Campanula rotundifolia</i>		2	1	1		1	2 ⁶		3
<i>Cladonia crispata</i>			2	1			2	6 ¹⁷	1
<i>Cladonia polycarpoides</i>			2	1		5 ¹¹	1		4
<i>Climacium dendroides</i>		10 ²⁴	1	1	1		5 ¹⁶		
<i>Knautia arvensis</i>			2	1				7 ²⁴	
<i>Rumex acetosella</i>		6 ¹⁷	1	2	1		2		4 ⁹
<i>Trifolium arvense</i>			1	1			6 ¹⁷	2	
<i>Veronica chamaedrys</i>		21 ³⁸	1	1			1	1	
<i>Cladonia uncialis</i>			1					3 ⁴	9 ²³
<i>Veronica spicata</i>			1	1				6 ²²	
<i>Petasites spurius</i>			1	2		1	1	4 ¹⁴	
<i>Cladonia foliacea</i>			1		3		6 ¹⁶		
<i>Equisetum arvense</i>		3	1	1			1	4 ¹⁴	
<i>Pimpinella saxifraga</i>		4	1	1			1	4 ¹⁵	
<i>Cladina portentosa</i>			1			1	2	3 ⁵	4 ¹⁰
<i>Viola</i> sp.		2	1	1		1	3 ¹⁰		1
<i>Pohlia</i> sp.			1	1		4 ¹⁸			
<i>Vicia</i> sp.			1	2			1	1	6 ¹⁷
<i>Melampyrum sylvaticum</i>			1	1				4 ¹⁸	
<i>Dicranum polysetum</i>			1	1			2	1	5 ¹⁵
<i>Equisetum hyemale</i>		1	1	1		1		3 ¹³	
<i>Bryum argenteum</i>			1	1	1	1	1	1	
<i>Cladonia sulphurina</i>			1					4 ¹⁷	1
<i>Bryum</i> sp.			1	2 ⁷	3	1	1		
<i>Phragmites australis</i>			1	1				4 ¹⁷	
<i>Centaurea scabiosa</i>			1		1			4 ¹⁷	
<i>Melampyrum pratense</i>		1	1	1	1	1	1	2 ⁸	
<i>Rumex acetosa</i>		5 ¹⁸	1	1			1	1	
<i>Oenothera rubricaulis</i>			1	1				3 ¹⁶	
<i>Rosa rugosa</i>			1	1	1			3 ¹³	
<i>Poa pratensis</i>		3	1	1	1		2 ⁹		
<i>Vaccinium vitis-idaea</i>			1	1				3 ¹⁶	
<i>Acer platanoides</i>			1	1				3 ¹⁵	
<i>Fulgensia bracteata</i>			1	1		3 ¹⁴			
<i>Potentilla argentea</i>		2	1	1	1		1	2 ¹²	
<i>Elytrigia repens</i>		2	1	1	1	1	1	2 ⁹	
<i>Rhinanthus apterus</i>			1				4 ¹⁷		
<i>Vicia cracca</i>		1	1	1				2 ¹¹	
<i>Erigeron acris</i>			1		1			2 ¹¹	
<i>Peltigera</i> sp.		1	1	2 ⁷	1	1		1	
<i>Verrucaria nigrescens</i>			1			2 ¹⁴		2 ¹¹	
<i>Juniperus communis</i>			1			1			
<i>Brachythecium salebrosum</i>		1	1	1			3 ¹⁵		
<i>Helictotrichon pubescens</i>			1				3 ¹⁷		
<i>Verrucaria calciseda</i>			1			2 ¹⁴			
<i>Luzula campestris</i>			1				1	2 ¹³	
<i>Erodium cicutarium</i>		7 ²²	1		1 ¹¹				
<i>Cladonia pocillum</i>			1			2 ¹³			
<i>Peltigera malacea</i>			1					2 ⁷	2
<i>Plantago lanceolata</i>		7 ²¹	1	1			1	1	
<i>Agrostis tenuis</i>		3 ¹⁴	1	1			1		1
<i>Hypochoeris radicata</i>		1	1	1			1	1 ⁹	
<i>Lerchenfeldia flexuosa</i>			1				1	1 ⁹	
<i>Stellaria graminea</i>		9 ²⁵	1					1	
<i>Sagina nodosa</i>			1	1				1 ⁹	
<i>Brachythecium velutinum</i>			1	1	1		1	1	
<i>Pyrola rotundifolia</i>		2	1	1		1		1	

Assoc. 1. Assoc. 2 Assoc. 3 Var. 3.1. Var. 3.2. Var. 3.3. Var. 3.4. Var. 3.5. Var. 3.6.

<i>Sorbus aucuparia</i>		1	1				2 ¹¹	
<i>Cephaloziella rubella</i>		1				1		3 ¹³
<i>Peltigera polydactyla</i>	1	1		2 ⁸		1		
<i>Betula pendula</i>		1					2 ¹²	
<i>Cladonia bacillaris</i>		1				1		4 ¹⁸
<i>Brachythecium oedipodium</i>		1	1		1	1		
<i>Conyza canadensis</i>		1					2 ¹²	
<i>Linaria loeselii</i>		1	1		1		1	
<i>Cladonia rei</i>		1	1		1			3 ¹⁴
<i>Tortula obtusifolia</i>		1		2 ¹²				
<i>Vicia hirsuta</i>	1	1		1			2 ¹¹	
<i>Pseudevernia furfuracea</i>		1				1	1	
<i>Hylocomium splendens</i>		1	1		1	1	1	1
<i>Orchilina secunda</i>	1	1						1 ¹¹
<i>Cladina ciliata</i>		1	1				2 ⁹	1

Additional species: *Acarospora veronensis* 3.3.:1, *Achyroporus maculatus* 3.5.:1, *Acinos arvensis* 3.1.:1, *Agrimonia eupatoria* 3.5.:1, *Agrostis stolonifera* 3.1.:1, *Allium* sp. 3.2.:1, *Alnus incana* 3.5.:1, *Amblystegium serpens* 3.1.:1, 3.4.:1, *Antennaria dioica* 3.4.:1, *Anthoxanthum odoratum* 3.4.:1, *Anthriscus sylvestris* 2.:1, 3.5.:1, *Arenaria serpyllifolia* 2.:1, 3.4.:1, *Artemisia absinthium* 3.1.:1, 3.2.:1, *Artemisia vulgaris* 3.5.:1, *Asparagus officinalis* 3.1.:1, 3.2.:1, 3.5.:1, *Astragalus danicus* 3.3.:1, *Barbula unguiculata* 3.3.:1, *Berteroa incana* 2.:1, 3.2.:1, 3.4.:1, 3.5.:1, *Biatora* sp. 3.6.:1, *Botrychium virginianum* 3.3.:1, *Brachythecium rutabulum* 3.1.:1, 3.2.:1, 3.4.:1, *Bryum caespiticium* 3.3.:1, 3.5.:1, *Bryum capillare* 3.1.:1, 3.4.:1, *Bryum pseudotriquetrum* 3.5.:1, 3.6.:1, *Bryum subelegans* 3.3.:1, 3.5.:1, *Cakile baltica* 3.1.:1, 3.3.:1, 3.5.:1, *Calliergon cordifolium* 2.:1, 3.1.:1, *Calliergon* sp. 3.1.:1, *Calliergon stramineum* 2.:5, *Calliergonella cuspidata* 3.6.:1, *Caloplaca citrina* 3.3.:1, *Caloplaca lactea* 3.3.:1, *Campanula patula* 3.5.:1, *Campanula persicifolia* 3.5.:1, *Candelariella vittelina* 3.3.:1, *Capsella bursa-pastoris* 2.:1, 3.5.:1, *Carex hirta* 2.:1, *Centaurea jacea* 3.5.:1, *Centaureum littorale* 3.4.:1, *Cephalanthera rubra* 3.3.:1, *Cephalozia bicuspidata* 3.1.:1, 3.3.:1, 3.4.:1, 3.6.:1, *Cerastium holosteoides* 3.5.:1, *Cerastium* sp. 2.:1, *Cetraria* sp. 3.1.:1, 3.3.:1, *Chamaenerion angustifolium* 3.5.:1, *Chelidonium majus* 3.1.:1, *Chenopodium rubrum* 3.1.:1, *Chimaphila umbellata* 3.5.:1, *Cirsium arvense* 3.1.:1, *Cladina* sp. 2.:1, 3.1.:1, 3.2.:1, *Cladonia botrytes* 3.6.:1, *Cladonia cariosa* 3.1.:1, 3.5.:1, 3.6.:1, *Cladonia cenotea* 3.6.:3, *Cladonia grayi* 3.1.:1, *Cladonia ramulosa* 3.1.:1, 3.3.:1, 3.6.:3, *Cladonia symphylicarpa* 3.5.:1, *Convallaria majalis* 3.5.:1, *Convolvulus arvensis* 3.1.:1, *Corispermum intermedium* 3.3.:1, *Dactylis glomerata* 2.:1, 3.1.:1, 3.5.:1, *Dianthus deltoideus* 2.:1, 3.1.:1, 3.5.:1, 3.6.:1, *Dicranoweisia crispula* 3.3.:1, *Dicranum bergeri* 3.5.:1, *Dicranum majus* 3.1.:1, 3.4.:1, *Dicranum montanum* 3.5.:1, *Dicranum* sp. 3.1.:1, 3.3.:1, *Dicranum spurium* 3.4.:1, *Diplotoma epipolium* 3.3.:1, *Eleagnus argentea* 3.1.:1, 3.5.:1, *Epipactis helleborine* 3.5.:1, *Eryngium maritimum* 3.3.:1, *Euphorbia cyparissias* 3.5.:1, *Euphrasia parviflora* 3.5.:1, *Euphrasia* sp. 2.:2, 3.5.:1, *Eurhynchium hians* 3.1.:1, *Evernia divaricata* 3.3.:1, *Festuca ovina* 3.4.:1, *Festuca rubra* 2.:3, *Filipendula ulmaria* 3.5.:1, *Fragaria vesca* 3.1.:1, 3.5.:1, *Fragaria viridis* 3.1.:1, 3.5.:1, *Frangula alnus* 3.5.:1, *Fraxinus excelsior* 3.5.:1, *Funaria hygrometrica* 3.3.:1, 3.5.:1, *Galeopsis tetrahit* 3.1.:1, 3.5.:1, *Galium palustre* 3.5.:1, *Geranium pusillum* 3.1.:1, *Geranium sanguineum* 3.5.:1, *Helictotrichon pratense* 3.5.:1, *Holcus lanatus* 3.5.:1, *Holcus* sp. 2.:1, 3.1.:1, 3.4.:1, *Homalothecium lutescens* 3.5.:1, *Hypericum maculatum* 3.5.:1, *Hypericum perforatum* 3.5.:1, *Hypericum* sp. 2.:4, 3.4.:1, *Hypogymnia farinacea* 3.1.:1, *Juncus articulatus* 3.1.:1, 3.5.:1, *Juncus balticus* 2.:1, 3.1.:1, 3.5.:1, *Juncus bufonius* 3.5.:1, *Juncus effusus* 3.5.:1, *Juncus* sp. 3.1.:1, 3.5.:1, *Lathyrus pratensis* 3.5.:1, *Lathyrus sylvestris* 3.5.:1, *Lecanora rupicola* 3.3.:1, *Lecidella* sp. 3.3.:1, *Lecidella stigmatea* 3.3.:1, *Leontodon hispidus* 2.:4, 3.5.:1, *Leucanthemum vulgare* 3.5.:1, *Lonicera caerulea* subsp. *pallasii* 3.3.:1, *Lophozia* sp. 3.1.:1, 3.4.:1, *Lotus corniculatus* 3.1.:1, 3.4.:1, *Luzula multiflora* 3.3.:1, *Luzula* sp. 2.:1, 3.1.:1, 3.5.:1, *Lycopodium clavatum* 3.5.:1, *Malus* sp. 3.5.:1, *Medicago lupulina* 2.:1, 3.1.:1, 3.4.:1, 3.5.:1, *Medicago* sp. 2.:1, *Melampyrum nemorosum* 3.5.:1, *Nardus stricta* 3.5.:1, *Ochrolechia androgyna* 3.6.:1, *Odontites vulgaris* 2.:1, *Parmelia sulcata* 3.1.:1, 3.2.:2, 3.4.:1, *Picea abies* 3.5.:1, *Pinus montana* 3.5.:1, *Placynthiella* sp. 3.1.:1, 3.3.:1, *Placynthiella uliginosa* 3.6.:1, *Plagiomnium affine* 2.:2, 3.1.:1, 3.4.:1, 3.5.:1, *Platismatica glauca* 3.6.:1, *Poa annua* 2.:1, *Poa* sp. 3.1.:1, *Polygonatum odoratum* 3.5.:1, *Polygonum* sp. 2.:1, *Polypodium vulgare* 3.5.:1, *Populus tremula* 3.5.:1, *Potentilla anserina* 3.1.:1, 3.5.:1, *Potentilla arenaria* 3.1.:1, 3.4.:1, *Prunus* sp. 3.1.:1, *Ptilidium pulcherrimum* 3.5.:1, *Pyrola* sp. 3.3.:1, *Quercus robur* 3.5.:1, 3.6.:1, *Ranunculus acris* 2.:3, 3.4.:1, *Ranunculus bulbosus* 2.:1, 3.1.:1, 3.4.:1, *Rhinanthus minor* 3.5.:1, *Rhinanthus* sp. 3.5.:1, *Rhizocarpon obscuratum* 3.3.:1, *Rhytidadelphus squarrosus* 2.:3, *Rhytidadelphus triquetrus* 3.5.:1, *Rubus caesius* 3.5.:1, *Rumex crispus* 2.:1, 3.4.:1, *Sagina procumbens* 2.:1, *Salix cinerea* 3.1.:1, 3.5.:1, *Salix* sp. 3.1.:1, 3.5.:1, *Salix viminalis* 3.5.:1, *Saponaria officinalis* 3.5.:1, *Scorzonera humilis* 3.4.:1, 3.5.:1, *Selinum carvifolia* 3.5.:1, *Senecio vernalis* 3.1.:1, 3.2.:1, *Sieglingia decumbens* 2.:1, 3.3.:1, 3.4.:1, *Sonchus arvensis* 3.1.:1, *Stereocaulon condensatum* 3.6.:1, *Stereocaulon tomentosum* 3.3.:1, 3.6.:1, *Syringa vulgaris* 3.5.:1, *Tanacetum vulgare* 3.1.:1, 3.2.:1, 3.5.:1, *Tephromela atra* 3.3.:1, *Thymus ovatus* 3.5.:1, *Tortella inclinata* 3.3.:1, *Tortella tortuosa* 3.1.:1, 3.2.:1, 3.3.:1, *Tortula latifolia* 3.1.:1, *Tortula lingulata* 3.3.:1, *Tortula subulata* 3.1.:1, 3.2.:1, *Trifolium medium* 3.5.:1, *Trifolium pratense* 2.:1, *Trifolium repens* 2.:1, 3.4.:1, *Tussilago farfara* 3.5.:1, *Vaccinium myrtillus* 3.5.:1, *Veronica officinalis* 3.4.:1, *Verrucaria* sp. 3.3.:1, *Vicia lathyroides* 3.1.:1, 3.4.:1, *Vicia septium* 3.5.:1, *Xanthoparmelia somloensis* 3.1.:1, 3.5.:1, *Xanthoria parietina* 3.2.:1.

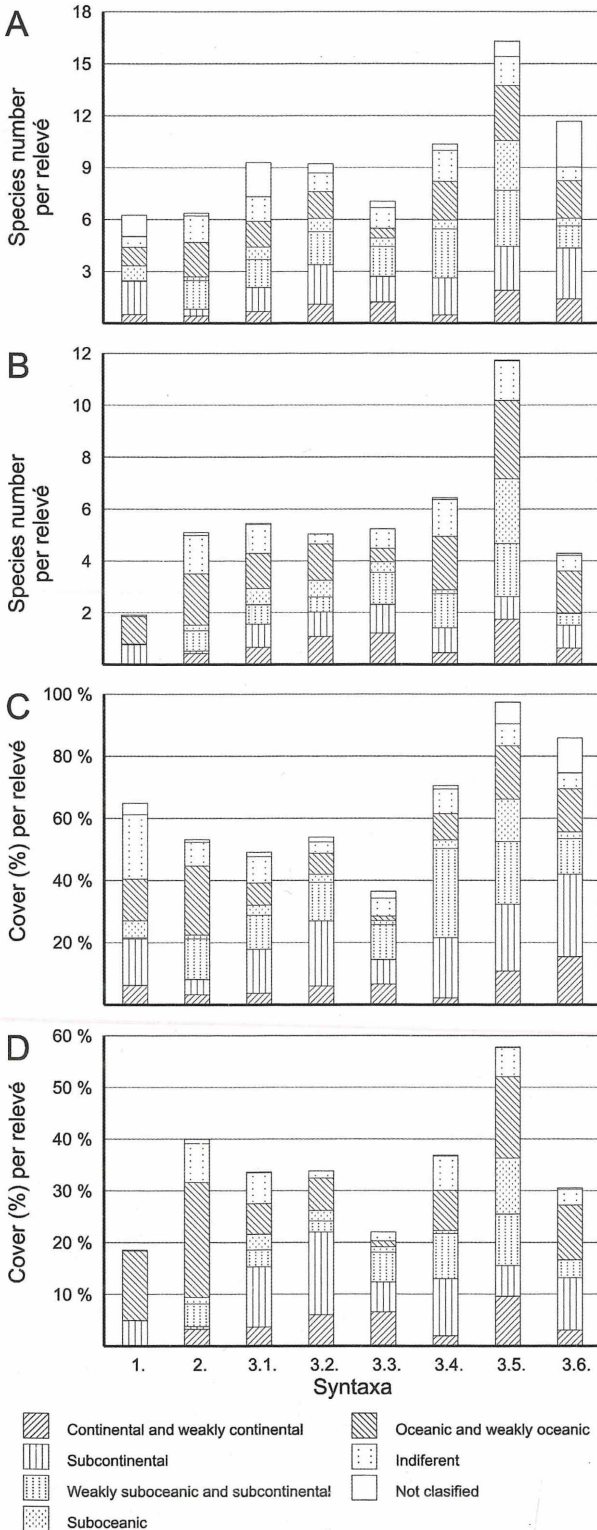


Fig. 2: Continentiality spectra of grey dune communities in Latvia based on different criteria. A: mean total plant species richness in the analysed relevés (plot size usually 1 m²); B: mean vascular plant species richness in the analysed relevés; C: mean cover (all plants); D: mean cover (only vascular plants). The figures denote the following communities:

1 - *Corniculario aculeatae-Corynephorum canescentis*, 2 - *Caricetum arenariae*, 3.1 - *Festucetum polesicae*, typical variant, 3.2 - *F. p.*, variant of *Gypsophila paniculata*, 3.3 - *F. p.*, variant of *Koeleria glauca*, 3.4 - *F. p.*, variant of *Thymus serpyllum*, 3.5 - *F. p.*, variant of *Epipactis atrorubens*, 3.6 - *F. p.*, variant of *Corynephorus canescens*.

Abb. 2: Kontinentalitätsspektren der Pflanzengesellschaften der Graudünen Lettlands nach verschiedenen Kriterien. A: mittlerer Artenreichtum (alle Pflanzengruppen) in den analysierten Aufnahmen (Fläche überwiegend 1 m²); B: mittlerer Artenreichtum (nur Gefäßpflanzen) in den analysierten Aufnahmen; C: mittlerer Deckungsgrad (alle Pflanzengruppen); D: mittlerer Deckungsgrad (nur Gefäßpflanzen). Für die Bedeutung der Gesellschaftsnummern siehe englische Abbildungsunterschrift.

Table 4: Chemical properties of mixed soil samples (uppermost 10 cm) from 10 grey dune sites. For the precise location of the sites, see Appendix A.

Tab. 4: Chemische Bodenparameter (Mischproben der obersten 10 cm) für 10 Graudünenstandorte. Die genauen Fundortangaben können Anhang A entnommen werden.

Location code	Location	Syntaxon	pH (H ₂ O)	pH (KCl)	N (%)	Ca (µg/g)
2	Nida	Assoc. 2	6.5	4.5	0.081	1,863
8	Pape	Var. 3.2	6.8	6.0	0.042	648
28	Pāvilosta	Assoc. 3	5.4	3.9	0.057	321
31	Užava	Var. 3.3	7.2	6.3	0.056	3,123
51	Lielirbe	Assoc. 3	6.0	4.6	0.014	1,121
62	Ģipka	Var. 3.1	5.4	4.2	0.056	81
78	Daugavgrīva	Var. 3.1	6.3	4.1	0.034	270
84	Lilaste	Var. 3.5	6.6	5.5	0.028	130
91	Šķīsterciems	Assoc. 2	6.8	4.7	0.000	6,053
96	Ainaži	Var. 3.1	6.9	5.9	0.114	3,536

burned, creating mobile sand areas without vegetation. However, the former land use has drastically decreased during the last 20–30 years. Many grey dunes have been overgrown with pine trees, shrubs or dense *Calamagrostis epigeios* stands, and only some sandy patches or belts on pathways develop periodically. As wind is a significant factor even for grey dunes, and considering that the dunes of Pāvilosta are situated towards the sea, the ecological preconditions are more or less favourable for the *Corynephorus canescens* habitat development. The *Corniculario-Corynephorum* typically colonises weakly acid to neutral soil without a humus layer or with a very thin one. A limiting factor for plants is the shingle-sandy soil substrate, which is easily leached.



Fig. 3: *Corniculario aculeatae-Corynephorum canescens* in Pāvilosta.

Abb. 3: *Corniculario aculeatae-Corynephorum canescens* in Pāvilosta.

4.2.2. *Caricetum arenariae*

The *Caricetum arenariae* comprises heterogeneous vegetation stands dominated by *Carex arenaria* (Fig. 4). The open stands, which are poor in plant species, represent pioneer vegetation, others are characterised by more closed vegetation. As a central association in the alliance *Corynephorion canescentis*, it lacks character species (DENGLER 2004). In younger succession stages, the plant cover is very sparse, and often *Carex arenaria* is accompanied by only 2–5 species, which are *Hieracium umbellatum*, *Calamagrostis epigeios*, *Festuca sabulosa*, *F. arenaria* and the moss *Brachythecium albicans* (Table 1 and Table 2 in the Supplement).

Physiognomically, the older successional stages sharply contrast with other communities and are characterised by dense and quite high vegetation (30–60 cm) dominated by *Carex arenaria*. The most abundant species has high occurrence (97%) and a cover of 40–70%. Other frequent species with low cover values are *Galium mollugo*, *Hieracium umbellatum*, *Sedum acre*, *Calamagrostis epigeios*, *Festuca arenaria*, the mesophilous grassland species *Achillea millefolium*, *Linaria vulgaris*, *Veronica chamaedrys* and the bryophytes *Brachythecium albicans*, *Pleurozium schreberi* and *Climacium dendroides*.

The pioneer stages of the *Caricetum arenariae* can be found on lee slopes of mobile dunes, as well as on dynamic seashores where primary dunes are washed out periodically. This community is distributed on dunes along the entire Latvian coast, but particularly on the coast of the Gulf of Rīga, where dune strengthening with *Ammophila arenaria* is limited because of a sand deficit.

Stands of the *Caricetum arenariae* with dense vegetation mostly occur in depressions and on leeward slopes. These sites are relatively humid, eutrophic and protected by dunes from sea wind and sand drift. Often, *Caricetum arenariae* is like a contact community between mesophytic grasslands and the *Festucetum polesicae* or even primary dunes with *Leymus arenarius*. The main localities of the older successional stages *Caricetum arenariae* are the widest dune areas of, e.g., Nida-Pape, Ziemupe, Pāvilosta and Rīga. These dunes were formerly grazed or cut, but during the last 20 years this land use has nearly stopped.



Fig. 4: *Caricetum arenariae* in Pāvilosta.

Abb. 4: *Caricetum arenariae* in Pāvilosta.

4.2.3. *Festucetum polesicae*

The *Festucetum polesicae* is characterised by high phytosociological diversity. Six variants with floristical and structural differences can be recognised (Table 1 and Table 3 in the Supplement). Vegetation coverage ranged from 38% to 100%, the mean coverage of the herb layer was 36%, of bryophytes 16% and of lichens 11%. Average vascular plant species richness per relevé was 6.7 species, of bryophytes 1.7 species, and of lichens 1.8 species. Diagnostic species are *Festuca sabulosa*, *Koeleria glauca*, *Tortula ruralis*, *Ceratodon purpureus* and *Dianthus arenarius*. The *Festucetum polesicae* often occurs adjacent to white dunes, forests or mesophytic grasslands. Therefore, in some cases the community contains white dune species like *Ammophila arenaria*, *Festuca arenaria* and *Leymus arenarius*, in other cases forest species like *Pinus sylvestris*.

The *Festucetum polesicae* occupies different grey dune habitats on sandy, sandy-gravel or sandy-pebble substrate. The community develops in stable secondary dune areas as well as in dynamic coastal zones. The association is widely distributed in all coastal sections in Latvia.

The six variants of the *Festucetum polesicae* can be divided into three groups: sub-oceanic, weakly sub-oceanic and sub-continental. The variant of *Epipactis atrorubens* belongs to the sub-oceanic group due to prevailing species as for example *Epipactis atrorubens*, *Honckenya peploides*, *Ammophila arenaria* and *Pulsatilla pratensis*. The weakly sub-oceanic group comprise the typical variant and the variant of *Thymus serpyllum*. Their sub-oceanicity is shown mainly by presence of species such as *Carex arenaria*, *Thymus serpyllum* and *Artemisia campestris*. The *Gypsophila paniculata* variant is very poor in plant species; dominant species are the sub-continental *Festuca sabulosa* and *Cladonia fimbriata* and the widespread *Ceratodon purpureus*. The variant of *Koeleria glauca* is the most continental variant, with *Astragalus arenarius*, *Koeleria glauca* and *Alyssum gmelinii* as typical species. These latter two variants and also *Festucetum polesicae* var. *Corynephorus canescens* are characterised as sub-continental.

Typical variant

This community has sparse vegetation with scattered growing tussocks of *Festuca sabulosa*, the most common species in the stands. The syntaxon has no differential species. The most frequent species are *Artemisia campestris*, *Carex arenaria*, *Hieracium umbellatum*, *Sedum acre* and *Tortula ruralis* (Table 1 and Table 3 in the Supplement). On drier and more stable dunes, *Brachythecium albicans* (constancy 80%, phi coefficient = 0.60), *Festuca sabulosa* (constancy 78%), and *Sedum acre* (constancy 77%, phi coefficient = 0.50), are dominant species, and *Koeleria glauca* is common. Close to the sea, low dunes are often poor in plant species and cover. *Festuca sabulosa* (constancy 87%), *Hieracium umbellatum* (constancy 64%) and *Carex arenaria* (constancy 63%) are common; in some locations *Tragopogon heterospermus* (constancy 20%) occurs. Average coverage of the vegetation was 49%. In some stands *Festuca sabulosa* occurs as a dominant. The typical variant of the *Festucetum polesicae* is a common plant community in all coast sections in Latvia.

Variant of *Gypsophila paniculata*

The main differential species is *Gypsophila paniculata* with high diagnostic value (constancy 68%, phi coefficient = 0.78). This plant forms large stands, 80–100 cm in height, and acts as an edificator (i.e. a dominant plant species that significantly changes soil properties of the habitat). Among vascular plants, *Erophila verna*, *Cerastium semidecandrum* and *Silene borys-thenica* are the differential species (Table 1 and Table 3 in the Supplement). The moss *Tortula ruralis* is dominating (constancy 75%; Fig. 5). Other frequent cryptogams are *Brachythecium albicans*, *Ceratodon purpureus*, *Cetraria ericetorum*, *Cladonia coniocraea* and *C. fimbriata*. The latter two species are considered as differential species. *Festuca sabulosa* and *Sedum acre* often grow in a moss and lichen carpet. The *Gypsophila paniculata* variant is more typical on dynamic dune complexes with intense sand drift. One of the most typical localities is on the southern coastal zone in Pape. This site is wind- and sun-exposed and bordered by high white dunes. Soil pH is 6.8 and Ca 648 µg/g (Table 4).



Fig. 5: *Festucetum polesicae*, variant of *Gypsophila paniculata*, in Pape.

Abb. 5: *Festucetum polesicae* in der Variante von *Gypsophila paniculata* in Pape.

Variant of *Koeleria glauca*

The variant of *Koeleria glauca* is the most continental variant, dominated by xerophilous vascular plants. Within the association, this variant has the sparsest vegetation (mean coverage of 39%). *Pulsatilla pratensis*, *Alyssum gmelinii* and *Astragalus arenarius* are the main differential species (Table 1 and Table 3 in the Supplement). South of Ventspils, *Dianthus arenarius* is widely distributed within the *Festucetum polesicae*. In some places, mainly on the coast in Užava, the so-called pebble desert occupies large areas where soil pH is 7.2 and calcium concentration 3,123 µg/g (Table 4). These grey dunes are adjacent to an eroding seashore, i.e., this seashore has a sand deficit. Such conditions are extremely unfavourable for plants. Hummocks and pillows are dominating with interspersed low plant carpets. Patches of *Arctostaphylos uva-ursi*, *Salix rosmarinifolia* and *Thymus serpyllum* are characteristic. The cryptogams *Diploschistes muscorum*, *Lecanora muralis*, *Ditrichum flexicaule*, *Ceratodon purpureus* and *Cladonia* species are typical. The communities of this variant occupy wider areas on old dunes and are distributed mainly on the open Baltic Sea coast and the Irbe Strait coast.

Variant of *Thymus serpyllum*

This variant is rich in mosses (mean cover value 25%), and *Hypnum cupressiforme* is a differential species (Table 1 and Table 3 in the Supplement). The grasses *Festuca sabulosa* and *Koeleria glauca*, the sedge *Carex arenaria* as well as *Galium mollugo* are abundant. Dominant cryptogams are *Hypnum cupressiforme*, *Brachythecium albicans*, *Ceratodon purpureus*, and *Cetraria aculeata*. Mosaic structure in the plant cover can be observed, especially during the flowering aspect of *Thymus serpyllum*. In some locations mesophytic plant species form small patches. This community represents the next succession stage after the *Corniculario-Corynephorretum*. The favourable status of these dune grassland communities depends greatly on dune management by grazing and hay cutting. The main localities of the *Thymus serpyllum* variant are on the coast north of Liepāja, where wide areas of open secondary dunes have remained.

Variant of *Epipactis atrorubens*

The variant of *Epipactis atrorubens* includes different vegetation stands with *Epipactis atrorubens*, *Jasione montana*, *Cardaminopsis arenosa* and *Silene nutans* as differential species (Table 1 and Table 3 in the Supplement). The average vascular plant species richness per relevé is 11.7 and the mean herb layer coverage 58%. In some sites, a few shrubs grow among herbaceous plants. The mean lichen coverage per relevé is 21%. Some of these vegetation stands are located in the forest-dune ecotone, which is very rich in plant species. Several species, including *Sedum acre*, *Leymus arenarius*, *Carex arenaria*, *Tortula ruralis* and *Brachythecium albicans*, have high occurrence and fidelity (phi coefficients of 0.45–0.64). Other stands are open and poor in plant species due to their location close to old white dunes or on grey dunes periodically disturbed by sand drift. *Tragopogon heterospermus*, *Anthyllis maritima*, *Pulsatilla pratensis*, *Cardaminopsis arenosa* and *Ammophila arenaria* are characteristic for this vegetation. Stands of the *Epipactis atrorubens* variant are widely distributed along the coast of the Gulf of Rīga and the Irbe Strait.

Variant of *Corynephorus canescens*

This variant represents a lichen-rich grey dune plant community, which develops in heterogeneous vegetation between patches of *Caricetum arenariae*, *Corniculario-Corynephorum* and the typical variant of the *Festucetum polesicae*. Many lichens of the genus *Cladonia* dominate: *C. glauca*, *C. cornuta*, *C. phyllophora*, *C. furcata* and *C. coccifera*, as well as *Cladina mitis* (Table 1 and Table 3 in the Supplement). The bryophyte cover is somewhat patchy, represented mainly by *Polytrichum piliferum*, *Racomitrium canescens*, *Ceratodon purpureus*, *Dicranum fuscenscens* and *Brachythecium albicans*. Among the vascular plants, *Koeleria glauca*, *Thymus serpyllum*, *Dianthus arenarius* and *Festuca sabulosa* are found often, but with low cover values.

4.3. Distribution of grey dune plant communities on the Latvian coast

The investigated five coastal sections of Latvia differ phytosociologically in relation to geomorphology, coastal processes, flora and coastal management (Fig. 1). The observed differences might be considered to be subjective as they consider the described relevés and not the real coverage of plant communities. However, considering the large data set (3,430 relevés) and its distribution among the coastal sections, we argue that the data are representative for the distribution of grey dune communities (*Koelerio-Corynephoretea*).

The typical variant of the *Festucetum polesicae* is a common plant community in all coastal sections in Latvia and comprises eurybiont xerophytic species such as *Festuca sabulosa*, *Hieracium umbellatum* and *Sedum acre*. The *Epipactis atrorubens* variant of the *Festucetum polesicae* is widespread with main localities along the coast of the Gulf of Rīga and the Irbe Strait. Some small areas of this community type are also found on the open Baltic Sea coast. The distribution of this variant is explained by the distribution of *Epipactis atrorubens* with main localities along the northwestern coast (C2) and along the Gulf of Rīga coast, particularly around Rīga (C4) (CEPURĪTE 2005). The largest occurrences of the *Epipactis atrorubens* variant are associated also with areas of boreal pine forest of more than 50 years of age, which can be expected as they form contact communities between foredune and forest.

The *Caricetum arenariae* is distributed along the entire Latvian coast except between Oviši and Kolka (C2). Stands of the *Elymo arenarii-Ammophiletum arenariae* Br.-Bl. & de Leeuw 1936 nom. cons. propos. are typical in the southern part of this section between Oviši and Mazirbe, where depositional processes dominate, as *Ammophila arenaria* is more common in areas of drifting sand. In the north part of the Irbe Strait Coast (C2), washout processes create local conditions unsuitable for *Carex arenaria*. Also in section I (C1) south of Liepāja and in section III (C3) north of Rīga the *Caricetum arenariae* is not so common because of wide primary dune development.

The main localities of the *Koeleria glauca* variant of the *Festucetum polesicae* are located on the open Baltic Sea coast, on stable, old grey dunes with periodic desiccation events. Parts of the localities are associated with specific geological patterns. For example, the Užava grey

dunes are located on the Litorina Sea terrace, where the sand, gravel and pebble layer is at least 5–6 m thick and the ground water deeper than 4–5 m (LAIME et al. 2007). Distribution of the *Thymus serpyllum* variant and the *Corynephorus canescens* variant of the *Festucetum polesicae* as well as the *Corniculario-Corynephorum canescentis* is associated with wide dune areas within settlements, where land-use was dominated by grazing and hay-cutting of dry grassland.

Within the *Festucetum polesicae*, the *Gypsophila paniculata* variant is found only on the south-eastern coast, as two of the differential species *Gypsophila paniculata* and *Silene borysthenica* occur only in this area (GAVRILOVA 1999, ANDRUŠAITIS 2003). *Gypsophila paniculata* can be considered as an edifier of grey dunes, particularly south of Pape close to the Lithuanian border (LAIME 2002, RUDŽITE 2004, 2006).

Of the studied coastal sections, the Nida-Cape Ovišrags Coast (C1) shows the highest grey dune diversity on the Baltic Sea coast (Fig. 1) mainly due to floristical features, former land use and the occurrence of wide grey dune areas.

5. Discussion

5.1. Phytosociological classification

The present classification of grey dune communities in Larvia shows that in general the distinguished syntaxa within *Koelerio-Corynephoretea* are similar to those in other countries of the Baltic Sea region and partly to those of north-western Europe. The main differences are related to ranges of the syntaxa and character species. The diagnostic value of character species is geographically limited, and there are geographical effects on fidelity and general, regional and local character species (WESTHOFF & VAN DER MAAREL 1978).

Following DENGLER (2001b, 2004), we assigned the plant community with *Corynephorus canescens* to the association *Corniculario-acuteatae-Corynephorum canescentis* (Syn. *Violo dunensis-Corynephorum canescentis* Boerboom 1960, *Spergulo morisonii-Corynephorum canescentis* (Tx. 1928) Libbert 1933 sensu auct.). BIERMANN (1999) has analysed the synsystematic classification of the *Violo-Corynephorum* for the North Sea coast. He concluded that often two subassociations have been distinguished in literature based on lichen species: “*typicum*” and “*cladonietosum*” Presently, Latvian coast grey dune vegetation of the *Corniculario-Corynephorum* has not been differentiated into variants or subassociations because of insufficient quantitative data. Compared with records of the *Corniculario-Corynephorum* from Denmark, Germany and Poland (BIERMANN 1999, DENGLER 2001, JUŠKIEWICZ-SWACZYNA 2009), the described stands on Latvian grey dunes are very poor in plant species, especially vascular plants, and the herb layer has a sparse cover. This vegetation structure is typical for dry acidic nutrient-poor *Corynephorus* grassland (HASSE & DANIELS 2006). The plant community with *Corynephorus canescens* on the Latvian coast is similar to the typical subassociation (from the initial phase to the *Cladina*-dominant stands) (BIERMANN 1999) and the subtype of *Cladonia arbuscula* ssp. *mitis* (JUŠKIEWICZ-SWACZYNA 2009). Also on the coast of Lithuania two variants, “*typicum*” and “*Cladonia* spp.”, have been described within the association *Violo-Corynephorum canescentis* (STANKEVIČIŪTE 2000). Vegetation data demonstrate differences of character taxa of the *Corniculario-Corynephorum* within the Baltic Sea region. *Spergula morisonii* and *Teesdalia nudicaulis* as character species of this association are typical for the south part of the region (DENGLER 2001, JUŠKIEWICZ-SWACZYNA 2009) and rare in continental sands of Lithuania (BALEVIČIENĖ 1991). On the east Baltic coast, on the other hand, where these species are rare, the *Corniculario-Corynephorum* is characterised by *Cetraria aculeata*, *Cladonia mitis*, *Polytrichum juniperinum* and *Pycnothelia papillaria*. These floristical features can be envisaged as local character species within the range of the *Corniculario-Corynephorum*.

Up to now, the Latvian inland dune vegetation with *Corynephorus canescens* was placed within the association *Helichryso arenarii-Jasionetum litoralis* Libbert 1940, which was classified in the alliance *Corynephorion canescentis* (RUSIŅA 2007). We observed that one of the largest populations of *Corynephorus canescens* is located in the Rīga region within a shooting range on inland sands, where bare sand areas developed periodically. Unfortunately, this

territory has not been phytosociologically studied yet. At present, it is not possible to generalise information on the *Corniculario-Corynephorum* in Latvia due to insufficient data on the phytosociological characteristics of inland and coastal dune areas.

There is a different view in phytosociological classification in Europe regarding the syntaxonomy of *Carex arenaria* vegetation. Often they are distinguished as a “community” or “derivate community” (POTT 1995, SCHAMINÉE et al. 1996, RODWELL 2000) and only in a few cases as the association *Caricetum arenariae* (DENGLER 2004, BOCH & DENGLER 2006). In Latvia, the *Carex arenaria* community has not been described previously as a separate syntaxon. As a dominant species of the inland dunes vegetation, *Carex arenaria*-dominated stands were included in the association *Helichryso-Jasionetum* (RŪSIŅA 2007). Our analysis shows that the *Carex arenaria* vegetation of grey dunes in Latvia is clearly distinguishable from other plant communities, and thus it is assigned to the association *Caricetum arenariae*. However, *Carex arenaria* has high occurrences also in other syntaxa of secondary and primary dunes, for example in the *Festucetum polesicae* or in the alliance *Ammophilion arenariae* (Br.-Bl. & Tx. 1952) Schaminée et al. 1998, as well as in microhabitats where the succession from the *Corynephorus* grassland to the *Calluna vulgaris* communities occurs.

In xerophytic grasslands of Latvia, previously four plant communities within the alliance *Koelerion glaucae* had been described: *Poetum compressae* Kizienė 1928, *Festucetum polesicae*, *Koeleria glauca* community, *Silene otites-Koeleria glauca* community (RŪSIŅA 2007). However, for each of these only a limited number of localities were found; for example, *Festucetum polesicae* was characterised with 11 relevés. In the present study of grey dunes, the association *Festucetum polesicae* appeared to be very widespread and highly diverse along the coast. Of the six distinguished variants, the typical and the *Gypsophila paniculata* variant might be better treated as subassociations, and the variants of *Thymus serpyllum* and *Corynephorus canescens* included in the *Festucetum polesicae typicum*. The variant of *Epipactis atrorubens* should be considered in relation to dry pine forests and primary dunes, and the *Koeleria glauca* variant more with inland dunes and other similar coastal communities. The position of these syntaxa in the alliance *Koelerion glaucae* needs further study in Latvia as well as across the distributional range of the association, particularly considering the spatial and temporal continuum of grey dune vegetation.

The association *Festucetum polesicae* as a sub-continental community is distributed along the Baltic Sea coast from Denmark to southern Finland (DOLNIK 2003, DENGLER 2004, BOCH & DENGLER 2006, LÖBEL & DENGLER 2008). The general character species of the *Festucetum polesicae* are *Festuca sabulosa* and *Koeleria glauca*. The latter, a continental and less psammophytic element than *Festuca sabulosa*, is rare on some coastal areas, for example on the Curonian Spit (DOLNIK 2003). In Latvia the *Festucetum polesicae* community is similar to that in other countries. However, the spectrum of distinguished variants shows that in Latvia this association is phytosociologically more diverse than in other regions. The best resemblance is observed to the Estonian island Saaremaa, where additionally *Dianthus arenarius* and *Alyssum gmelinii* ssp. *gmelinii* were distinguished as character species of this association (BOCH & DENGLER 2006). These two species as regional character species show features of the eastern part of the West Baltic geobotanical subprovince (LAASIMER 1959).

The association *Helichryso-Jasionetum* of the alliance *Koelerion glaucae*, which is described for the Baltic Sea coast from Germany to Estonia (STANKEVIČIŪTE 2000, DENGLER 2001b, DOLNIK 2003, DENGLER 2004, BOCH & DENGLER 2006, LÖBEL & DENGLER 2008), has not been identified often in Latvia and was considered in the alliance *Corynephorion canescentis* (RŪSIŅA 2007). In Poland, however, it is placed in the alliance *Koelerion albescentis* of the order *Corynephoretalia canescentis* (MATUSZKIEWICZ 1981). The above differences in interpretation might arise from unclear diagnostic values according to vegetation structure, ecology and typical plant species composition. In our study we have not identified this association in grey dune communities, but our work in other habitats has suggested that some dry meadow plant communities can be designated as *Helichryso-Jasionetum*.

5.2. Phytogeographical features of the *Koelerio-Corynephoretea* communities on the Latvian coast

Fixed coastal dunes with herbaceous vegetation ('grey dunes') are mainly associated with syntaxa from the class *Koelerio-Corynephoretea* (EUROPEAN COMMISSION 2007). Although the communities of this class are distributed in the temperate and boreal zone of Europe (MUCINA 1997), highest diversity on the community level is characteristic for the North Sea and the Baltic Sea regions (DENGLER 2001a, 2003, 2004, RŪSIŅA 2007). Along the Baltic Sea coast from Germany eastwards, sub-continental and continental plant species become more important because of a change from oceanic to more continental climatic conditions (HOUSTON 2008). The largest dune areas with oceanic-suboceanic plant communities of the *Corynephorion canescentis* are found in Denmark, Germany and in the southern part of Sweden. *Koelerion glaucae* communities are distributed on the Baltic coast from Denmark to Finland and represent more sub-continental and continental vegetation (DIERBEN 1996, DENGLER 2004).

The two *Corynephorion canescentis* associations described in grey dunes of Latvia are the most oceanic compared with other distinguished syntaxa within this study. The *Caricetum arenariae* has a more oceanic character, whereas the *Corniculario-Corynephoretum* has a sub-oceanic to sub-continental character (Fig. 2). In Europe, this syntaxon is distributed mainly in oceanic regions of the temperate zone (KETNER-OOSTRA 2001, POTT 1995). Scattered coastal populations of *Corynephorus canescens* occur in southern Norway, Sweden and the eastern Baltic as far north as Riga (BLUNT 2006). The main distribution areas of *Corynephorus canescens* in Latvia are located in the southwest part and in the Riga region, with the largest populations in the inland dunes and the sands (KABUCIS 2000, ANDRUŠAITIS 2003). On the Latvian coast, stands of *Corniculario-Corynephoretum* dominated by *Corynephorus canescens* and without lichens were found only in small areas at times. In the *Corniculario-Corynephoretum*, sub-continental and weakly continental lichen species frequently dominate: *Cladonia gracilis*, *C. furcata*, *Cetraria islandica* and *Cladina mitis*, as well as sub-continental *Festuca sabulosa*. Probably in Latvia the *Corniculario-Corynephoretum* has a weakly sub-continental character compared to oceanic communities in central and western Europe. The *Festucetum polesicae* of the Latvian coast represents mainly a sub-continental community, except the sub-oceanic variant of *Epipactis atrorubens*. The phytogeographical analysis of the grey dune communities indicates weakly sub-continental vegetation on the Latvian coast.

5.3. Conservation of grey dune plant communities on the Latvian coast

Grey dunes are important in conservation of threatened species, as 15 vascular plant and seven lichen species included in the Red Book of Latvia (ANDRUŠAITIS 1996, 2003) are found in this habitat. Several plant species with distribution ranges limited to the Baltic Sea region are common on the Latvian coast, for example *Anthyllis maritima*, *Dianthus arenarius* subsp. *arenarius* and *Tragopogon heterospermus*. Grey dunes of Latvia are one of the main habitats for *Dianthus arenarius* subsp. *arenarius*, which is included in the EU Habitat Directive. Not only protection, but also the unified monitoring for this species in all countries is necessary. Conservation of coastal dunes is very important for the protection of littoral plant species. European initiatives to protect threatened coastal species are hopelessly insufficient (VAN DER MAAREL & VAN DER MAAREL-VERSLUYS 1996).

In Latvia, the coastal protection belt of the Baltic Sea and the Gulf of Riga is divided into a 300 m zone landwards as well as seawards. The largest grey dune areas are located in 15 Specially Protected Nature Territories, 14 of which are included in the Natura 2000 site network. Unfortunately, the protection regime of these areas is not sufficiently strict. Many grey dune areas are being destroyed due to a rapid increase in tourism, including ecotourism. The biological diversity of grey dunes is intrinsically linked to human activity. A low level of disturbance increases diversity, while heavy disturbance destroys dune vegetation (SERVANE et al. 2003). Specific management for grey dunes is very important for the Kurzeme Coast, where the *Corniculario-Corynephoretum* and the *Thymus serpyllum* variant of the *Festucetum polesicae* are distributed (Fig. 1). Loss of traditional grazing management is one of the most important impacts to be considered in conservation of these communities.

Plant communities can be used as indicators of environmental quality (ESPEJEL et al. 2004). Grey dunes are included in monitoring of protected coastal habitats, plant species and Natura 2000 territories. The preliminary result of coastal monitoring in Latvia shows a need for more detailed interpretation of grey dune habitats. As this monitoring is to a large extent based on vegetation, it is important to describe diagnostic features (vegetation structure, species) not only at association, but also subassociation and variant levels. Plant communities are important as mapping units in development of coastal protection and management plans. In this case, the plant communities need to be clearly defined and recognisable in the field. In conservation of biological diversity in the European Union, knowledge of plant communities along the Baltic coast can aid in interpretation of habitats types in the boreal biogeographical region (EUROPEAN COMMISSION 2007).

5.4. Concluding remarks

The paper provides a preliminary overview of grey dunes and their plant communities in Latvia, but does not provide a detailed review of classification of *Koelerio-Corynephoretea* vegetation in Latvia. The identified diagnostic species presently refer only to the local data set. Further work is needed to provide more plant community descriptions and to investigate their relations at national, Baltic geobotanical province and Baltic Sea region levels.

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Appendix A: Location, sampling year and plot size of the relevés

Locations marked with an asterisk refer to extended coastal sections, along which sampling took place. In these cases, starting and end points are given.

Anhang A: Herkunft, Jahr und Größe der verwendeten Vegetationsaufnahmen. Mit * gekennzeichnete Gebiete bezeichnen ausgedehntere Küstenabschnitte, entlang welcher Aufnahmen angefertigt wurden. Für diese sind jeweils Start- und Endpunkt angegeben.

Location code	Location	Latitude	Longitude	Latitude	Longitude	Year	Plot size (m ²)
1	Nida	56° 06' 00.6"	21° 03' 07.5"			2003	1
2	Nida	56° 06' 08.1"	21° 03' 04.7"			2006	1
3*	Nida – Pape	56° 04' 47.3"	21° 02' 41.2"	56° 08' 45.4"	21° 01' 42.3"	1995	1
4	Nida	56° 06' 08.1"	21° 03' 04.7"			2003	1
5	Nida	56° 06' 08.1"	21° 03' 04.7"			2004	1
6	Nida	56° 06' 08.1"	21° 03' 04.7"			2005	1
7	Pape	56° 08' 46.8"	21° 01' 40.6"			2002	1
8	Pape	56° 08' 46.8"	21° 01' 40.6"			2007	1
9	Pape	56° 10' 52.9"	21° 00' 20.0"			1994	1
10	Pērkone	56° 27' 13.4"	21° 00' 04.9"			2003	1
11	Pērkone	56° 27' 13.4"	21° 00' 04.9"			2004	1
12	Pērkone	56° 27' 13.4"	21° 00' 04.9"			2005	1
13*	Bernāti	56° 21' 53.3"	20° 58' 18.2"	56° 22' 38.9"	20° 58' 29.2"	1995	1
14	Šķēde	56° 36' 30.7"	21° 01' 34.6"			2003	1
15	Šķēde	56° 36' 30.7"	21° 01' 34.6"			2004	1

Location code	Location	Latitude	Longitude	Latitude	Longitude	Year	Plot size (m ²)
16	Šķēde	56° 36' 30.7"	21° 01' 34.6"			2005	1
17	Šķēde	56° 36' 34.6"	21° 01' 37.2"			2003	1
18	Šķēde	56° 36' 34.6"	21° 01' 37.2"			2004	1
19	Šķēde	56° 36' 34.6"	21° 01' 37.2"			2005	1
20*	Ziemeupe – Akmensrags	56° 44' 40.1"	21° 03' 35.4"	56° 49' 52.0"	21° 03' 22.7"	2000	1
21	Ziemeupe	56° 46' 56.6"	21° 03' 31.3"			2003	1
22	Ziemeupe	56° 46' 56.6"	21° 03' 31.3"			2004	1
23	Ziemeupe	56° 46' 56.6"	21° 03' 31.3"			2005	1
24	Akmensrags	56° 49' 25.3"	21° 03' 11.3"			2004	1
25	Akmensrags	56° 49' 34.0"	21° 03' 12.4"			2001	1
26	Pāvilosta	56° 53' 13.6"	21° 09' 53.6"			1995	1
27	Pāvilosta	56° 53' 13.6"	21° 09' 53.6"			2004	1
28	Pāvilosta	56° 53' 13.6"	21° 09' 53.6"			2006	1
29	Pāvilosta	56° 53' 13.6"	21° 09' 53.6"			2007	1
30	Pāvilosta	56° 53' 13.6"	21° 09' 53.6"			2008	1
31	Užava	57° 10' 05.9"	21° 24' 30.3"			2007	1
32	Užava	57° 10' 53.4"	21° 24' 36.7"			2003	1
33	Užava	57° 10' 53.4"	21° 24' 36.7"			2004	1
34	Užava	57° 14' 28.4"	21° 24' 48.3"			1995	1
35	Užava	57° 14' 28.4"	21° 24' 48.3"			2003	1
36	Užava	57° 14' 28.4"	21° 24' 48.3"			2004	1
37	Užava	57° 14' 28.4"	21° 24' 48.3"			2007	1
38*	Vārve – Ventspils	57° 15' 42.8"	21° 24' 48.4"	57° 22' 24.7"	21° 30' 49.4"	1995	1
39*	Oviši	57° 33' 17.1"	21° 41' 13.0"	57° 35' 50.0"	21° 51' 11.8"	1999	1
40*	Oviši – Lielirbe	57° 34' 27.3"	21° 43' 15.0"	57° 38' 18.6"	22° 07' 56.3"	1997	1
41	Lūžņa	57° 35' 53.8"	21° 52' 01.6"			2003	1
42	Lūžņa	57° 35' 53.8"	21° 52' 01.6"			2004	1
43	Lūžņa	57° 35' 53.8"	21° 52' 01.6"			2005	1
44	Ķesteri	57° 36' 55.5"	22° 02' 57.2"			2003	1
45	Ķesteri	57° 36' 55.5"	22° 02' 57.2"			2004	1
46	Ķesteri	57° 36' 55.5"	22° 02' 57.2"			2005	1
47	Lielirbe	57° 38' 17.4"	22° 07' 47.4"			1999	1
48	Lielirbe	57° 38' 17.4"	22° 07' 47.4"			2003	1
49	Lielirbe	57° 38' 17.4"	22° 07' 47.4"			2004	1
50	Lielirbe	57° 38' 17.4"	22° 07' 47.4"			2005	1
51	Lielirbe	57° 38' 17.4"	22° 07' 47.4"			2006	1
52	Jaunciems	57° 38' 49.1"	22° 09' 31.2"			1997	1
53	Mazirbe	57° 41' 25.9"	22° 19' 09.1"			1994	1
54	Saunags	57° 43' 27.9"	22° 26' 18.7"			1994	1
55	Kolka	57° 45' 20.1"	22° 34' 08.2"			2003	1
56	Kolka	57° 45' 20.1"	22° 34' 08.2"			2004	1
57	Kolka	57° 45' 30.0"	22° 36' 17.5"			1994	1
58	Kolka	57° 45' 30.0"	22° 36' 17.5"			2003	1
59	Kolka	57° 45' 30.0"	22° 36' 17.5"			2004	1
60	Kolka	57° 45' 30.0"	22° 36' 17.5"			2005	1
61	Melnšils	57° 39' 11.9"	22° 34' 50.5"			1995	1
62	Ģipka	57° 33' 51.2"	22° 40' 05.9"			2007	1
63*	Roja – Melnšils	57° 30' 33.1"	22° 48' 11.8"	57° 38' 18.9"	22° 35' 16.7"	2000	1
64	Roja	57° 30' 39.6"	22° 47' 56.6"			2003	1
65	Roja	57° 30' 39.6"	22° 47' 56.6"			2004	1
66	Roja	57° 30' 39.6"	22° 47' 56.6"			2005	1
67*	Upesgrīva – Valgalciems	57° 23' 26.3"	23° 00' 54.4"	57° 24' 35.8"	22° 57' 28.8"	1996	1
68*	Kaltene	57° 23' 13.5"	23° 01' 06.7"	57° 29' 48.5"	22° 49' 31.4"	2000	2
69*	Mērsrags – Upesgrīva	57° 21' 55.4"	23° 07' 19.9"	57° 22' 59.0"	23° 01' 25.1"	2000	2

Location code	Location	Latitude	Longitude	Latitude	Longitude	Year	Plot size (m ²)
70	Lepste	57° 17' 31.2"	23° 09' 46.6"			2005	1
71	Engure	57° 08' 44.4"	23° 13' 49.6"			2003	1
72	Engure	57° 08' 44.4"	23° 13' 49.6"			2004	1
73	Engure	57° 08' 44.4"	23° 13' 49.6"			2005	1
74*	Kēsterciems – Abragciems	57° 07' 02.2"	23° 14' 01.6"	57° 11' 49.4"	23° 12' 26.2"	2000	1
75	Ragaciems	57° 01' 13.4"	23° 30' 12.3"			2003	1
76*	Lapmežciems – Ragaciems	56° 59' 29.8"	23° 31' 45.5"	57° 02' 02.7"	23° 28' 39.7"	2000	2
77*	Jūrmala	56° 57' 52.3"	23° 37' 18.3"	57° 00' 16.5"	23° 55' 33.3"	1997	1
78	Daugavgrīva	57° 02' 26.9"	24° 00' 19.6"			2006	1
79*	Rīga – Kalngale	57° 02' 26.0"	24° 00' 17.8"	57° 05' 43.0"	24° 08' 48.8"	1998	1
80*	Kalngale – Carnikava	57° 05' 46.2"	24° 08' 54.7"	57° 09' 12.6"	24° 15' 10.5"	2000	1
81	Lilaste	57° 11' 22.3"	24° 19' 41.3"			2003	1
82	Lilaste	57° 11' 22.3"	24° 19' 41.3"			2004	1
83	Lilaste	57° 11' 22.3"	24° 19' 41.3"			2005	1
84	Lilaste	57° 11' 22.3"	24° 19' 41.3"			2007	1
85*	Saulkrasti	57° 14' 08.8"	24° 23' 39.4"	57° 15' 39.2"	24° 24' 31.1"	2000	1
86	Saulkrasti	57° 15' 29.3"	24° 24' 25.6"			2004	1
87*	Dunte – Liepupe	57° 22' 00.8"	24° 24' 05.4"	57° 27' 53.5"	24° 23' 12.3"	2000	2
88	Vitrupe	57° 38' 13.9"	24° 22' 24.8"			2003	1
89	Vitrupe	57° 38' 13.9"	24° 22' 24.8"			2004	1
90	Vitrupe	57° 38' 13.9"	24° 22' 24.8"			2005	1
91	Šķīsterciems	57° 39' 01.9"	24° 22' 10.1"			2006	1
92	Svētupe	57° 41' 37.8"	24° 21' 09.2"			2003	1
93	Svētupe	57° 41' 37.8"	24° 21' 09.2"			2004	1
94	Svētupe	57° 41' 37.8"	24° 21' 09.2"			2005	1
95*	Salacgrīva	57° 43' 57.6"	24° 20' 45.4"	57° 46' 55.4"	24° 20' 53.1"	2000	2
96	Ainaži	57° 51' 29.6"	24° 20' 48.1"			2007	1

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