

Flora and vegetation of the Wadden Sea islands and coastal areas

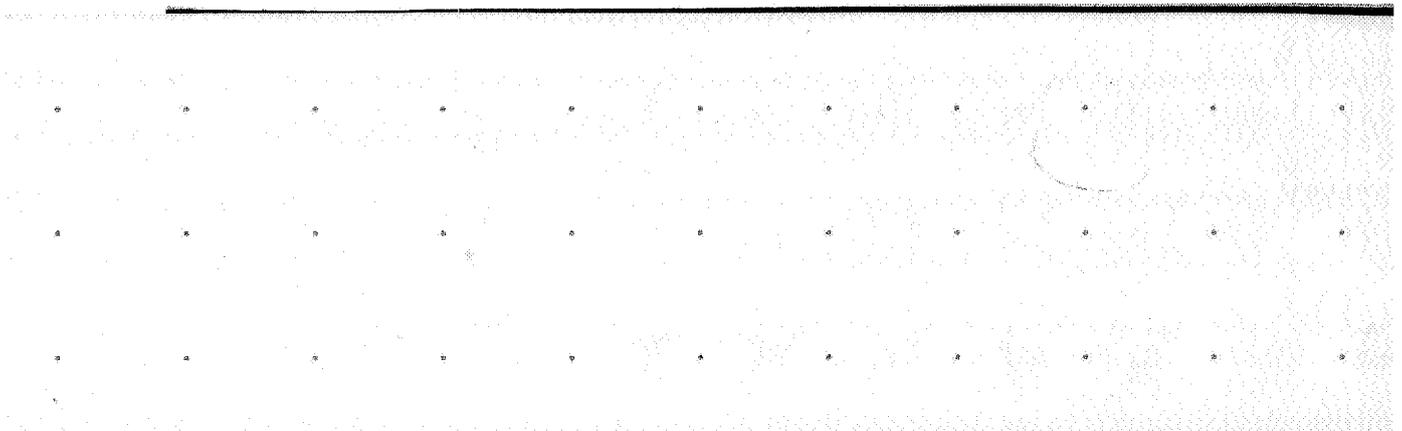
Report 9

*Final report of the section 'Flora and vegetation of the islands'
of the Wadden Sea Working Group*

edited by

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5.2 OUTLINE OF LANDSCAPE AND VEGETATION TYPES

K.S. Dijkema

In this chapter the syntaxonomic composition, the succession and distribution of the landscape and vegetation types mentioned in chapter 5.1 and shown on the vegetation map 1:100,000 are enumerated and described. Wherever possible the syntaxonomic classification of Westhoff & Den Held (1969) has been followed, but also use has been made of the references enumerated. In fig. 23 the principal succession series of the vegetation on mud flats, salt marshes, beach plains, dunes and dune slacks in the Wadden Sea area have been summarized according to this compiled references. This scheme was used to make a logical choice of colours for the map.

YELLOW-DUNE LANDSCAPE ("Weissdünen", "zeereep")

Ae Pioneer vegetation on embryonic dunes and nitrophilous vegetation

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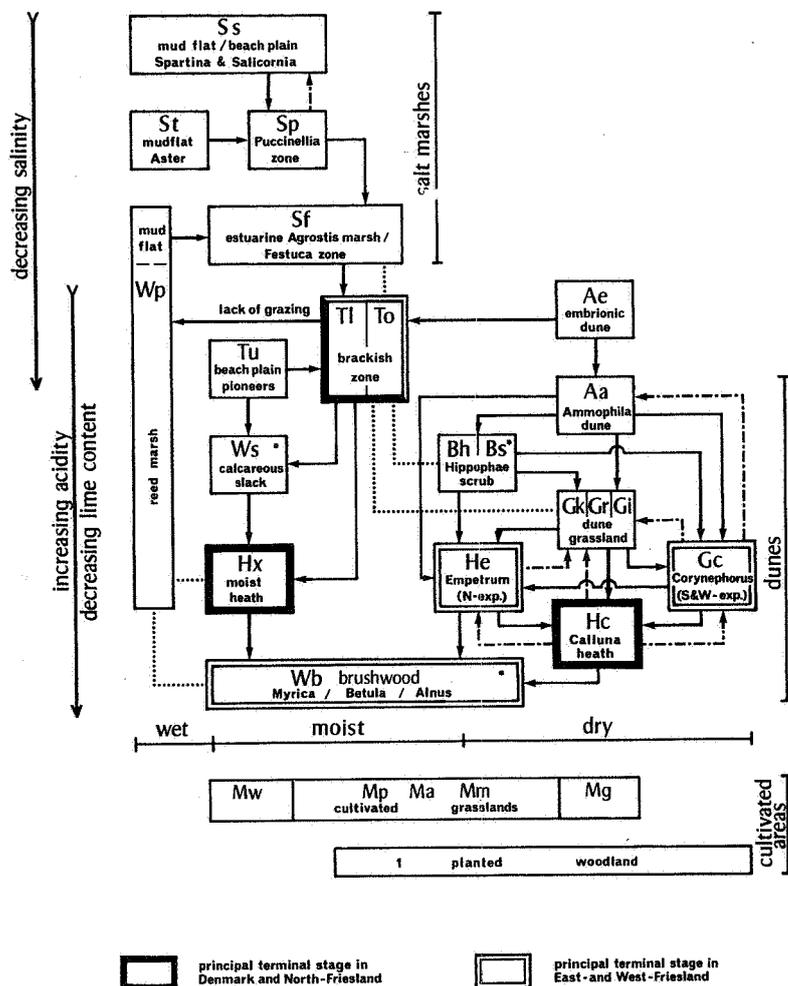


Fig. 23. Principal succession series on mud flats, salt marshes, beach plains, dunes and dune slacks in the Wadden Sea area. → succession; ← regression (by overgrazing, erosion, manuring); examples of zonations; * occurring on the East-Frisian and West-Frisian islands only.

with *Elymus farctus* (= *Agropyron junceum*) and *Elymus arenarius*.

Dominant communities - Cakiletum frasicum (Hoquette 1927) R.Tx. 1950, Agropyretum boreo-atlanticum (Warming 1909) Br.-Bl. et De Leeuw 1936 em. R.Tx. 1952 (synon.: Minuartio-Agropyretum juncei R.Tx. 1952 n.n.), Potentillo-Elymetum arenariae Raunkiaer 1935.

Succession - The Cakiletum ("Spülsaum-Gesellschaft") is a shortlived pioneer community on drift material overblown by sand. Sometimes it is succeeded by *Elymus farctus* subsp. *boreali-atlanticus* (= *Agropy-*

on

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ron junceum) ("Vordünen-Gesellschaft"), but the latter mostly occurs as a pioneer itself on embryonic dunes. When the embryonic dunes are sufficiently desalinated, a development to the Elymo-Ammophiletum (Aa) is possible.

On Rømø and Spiekeroog insufficient sand supply leads to succession of the Agropyretum by brackish grasslands with *Festuca rubra* and *Agrostis stolonifera* (To) (Wiemann & Domke, 1967; Wiinstedt, 1946).

Beaches on Rømø, Fanø and near Ordning show *Puccinellia maritima* (Sp) as a primary dune builder, succeeded by *Elymus farctus* (Heykena), 1965).

Distribution - On the islands and flats bordering the North Sea dune building takes place on some large parts of beaches. At most places, however, the coastal dune ridge is eroded by the sea.

The nitrophilous Potentillo-Elymetum occurs on the bird islands Jordsand, Norderoog, Scharhörn, Mellum, Memmert and Griend and at the Pleistocene border near Schobüll.

References - Bakker (1976): 85-104; Beeftink (1965): 135-138; Boerboom (1960): 14-16, 103, 104; Doing (1974): 32, 33, 35-37; Heykena (1965): 13-32; Runge (1973): 38, 48; Tüxen (1966): 358-362; Westhoff (1947): 68-70; Westhoff & Den Held (1969): 71-73, 101; Wiemann & Domke (1967): 205-237; Wiinstedt (1946): 311-313.

Aa Pioneer vegetation with *Ammophila arenaria* on the coastal dune ridge and on secondary windblown dunes.

Dominant community - Elymo-Ammophiletum (Warming 1909) Br.-Bl. et De Leeuw 1936 em. R.Tx. 1952.

Succession - At most places the coastal dune ridge is eroded by the sea and there the *Ammophila* dunes ("Helmdünen-Gesellschaft") border sharply on the beach, otherwise they succeed the Agropyretum (Ae). With decreasing overblow by sand the subassociation festucetosum takes over.

On calcareous dune sand (more than 0.3% lime; Westhoff, 1947) a *Hippophaë* scrub (Bh) appears. Mainly on S- and W-exposures dune grasslands (Gk) can develop too. Where limit content is relatively high, *Rubus caesius* is locally dominant on parabolic dunes.

On dune sand poor in lime or without lime (less than 0.3% lime; Westhoff, 1947) the succession leads from the Elymo-Ammophiletum to *Corynephorus* dunes (Gc) or directly to *Empetrum* heaths (Hc). Under the influence of grazing or manuring by birds dune grasslands (Gk) can develop too.

In dune landscapes wind erosion leads to secondary formation of the Elymo-Ammophiletum (wandering dunes).

Distribution - Occurring on the coastal dune ridge in the entire dune area, often too small to map.

Secondary windblown dunes are found especially on Sylt, Amrum, Nor-

derney, Schiermonnikoog and Vlieland.

References - Bakker (1976): 85-104; Boerboom (1960): 16-19; Doing (1974): 37-39; Heykena (1965): 38-40, 51-66, 101-103; Runge (1973): 39; Westhoff (1947): 70-76; Westhoff & Den Held (1969): 102, 103; Wiemann & Domke (1967): 237-285; Wiinstedt (1946): 311-313.

DUNE-SCRUB LANDSCAPE ("Dunen-Gebüsche", "duinstruwelen")

Bh Pioneer scrub with *Hippophaë rhamnoides* on young calcareous dunes and in the brackish zone.

Dominant community - *Hippophaë rhamnoides*-consociation Boerboom 1960.

Succession - On calcareous dunes (lime content and pH not under 0.3% resp. 6.0; Westhoff, 1947) at the East- and West-Frisian islands a *Hippophaë* scrub ("Sanddorn-Gebüsch") appears in the Elymo-Ammophiletum (Aa) and in the Tortulo-Phleetum (Gk).

Brackish low dunes on beach plains (To) are also grown with *Hippophaë* scrub, e.g. on Schiermonnikoog and Terschelling.

On N-exposures a decrease of the pH under 5.5 (Westhoff, 1947) leads to dwarf shrub vegetation (He, Gi) and on S- and W-exposures it leads to grey dunes (G).

Distribution - On the East- and West-Frisian islands, mainly on the lee-side of the coastal dune ridge; the better development on Texel, Ameland, Schiermonnikoog and the western East-Frisian islands is connected with the higher lime content of the dune sand there.

The dunes in the North-Frisian and Danish Wadden Sea area are almost free of lime and the lack of *Hippophaë* scrub is due to their rapid acidification.

References - Beeftink (1965): 142-145; Boerboom (1960): 51-59; Heykena (1965): 103-105; Sloet van Oldruitenborgh (1976): 70, 71; Westhoff (1947): 91-93.

Bs Scrub with *Sambucus nigra*, *Hippophaë rhamnoides* (and *Crataegus monogyna*) on young calcareous dunes.

Dominant community - *Hippophaë*-*Sambucetum* Boerboom 1960.

Succession - On sheltered places rich in organic matter and nutrients *Sambucus* ("Holunder-Busch") can appear in the *Hippophaë* scrub (Bh).

Distribution - As described under Bh. Optimum development on Texel.

References - Boerboom (1960): 65-69; Doing (1974): 67-69; Heykena (1965): 103-105; Runge (1973): 222; Sloet van Oldruitenborgh (1976):

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70-71; Westhoff (1947): 92; Westhoff & Den Held (1969): 242, 243.

GREY-DUNE LANDSCAPE ("Graudünen und Silbergrasfluren"; "duingraslanden")

The NW - to NE - slopes sometimes have a vegetation of greater density with dwarf shrubs and *Polypodium vulgare*.

Communities - Polypodio-Salicetum (R.Tx. 1955 n.n.) Boerboom 1960, Polypodio-Empetretum (Meltzer 1941) Westhoff 1947.

Gk Closed grasslands with *Agrostis tenuis*, *Carex arenaria*, *Festuca tenuifolia* (belonging to *F. ovina*), *Galium verum* and various mosses on dry dunes.

Dominant communities - Tortulo-Phleetum arenariaⁱ (Massart 1908) Br.-Bl. et De Leeuw 1936, Festuco-Galietum maritimi (Onno 1933) Br.-Bl. et De Leeuw 1936 (synon.: Agrostio-Poëtum humilis R.Tx. et Preisling 1951), Airo-Caricetum arenariae Westhoff, Van Leeuwen et Adriani 1962.

Succession - In older stabilized dunes the pH decreases by the leaching of lime and an increase of the humus content. The succession then leads from *Ammophila* dunes (Aa) or *Hippophaë* scrub (Bh) to dune grasslands ("Graudünen"). With a lime content of at least 0.2% and a pH of 7.0 - 6.3 (Westhoff, 1947) the intermediate stage is the Tortulo-Phleetum ("Sternmoos-Rasen").

Soil acidity in West- and East-Frisian dune grasslands is 7.3-5.4 pH and in North-Frisian and Danish dune grasslands it is 5.7-4.2 (Heykena, 1965; Westhoff, 1947). Further decrease of the pH can lead to *Corynephorus* dunes (Gc) or *Calluna* heaths (Hc).

The dune grasslands are maintained by grazing and manuring by rabbits, sheep and cattle or manuring by birds and under those circumstances they may develop on decalcified dunes too.

Grazing and treading in dune heaths (He, Hc) and manuring of *Corynephorus* dunes also lead to dune grasslands (Heykena, 1965).

Distribution - On stabilized, almost decalcified dry dunes in the entire area, mainly on S- and W-exposures. Dunes without lime need the influence of grazing, treading or manuring (e.g. near Nordby on Fanø, the Ellenbogen on Sylt, near Norddorf on Amrum, on Terschelling and Vlieland).

References - Boerboom (1960): 20, 21, 43-45; Doing (1974): 41-45, 50-52; Heykena (1965): 47, 66-72, 79, 80, 85, 106, 109, 121; Runge (1973): 154, 155; Westhoff (1947): 77-81, 84-87; Westhoff & Den Held (1969): 150, 155-157; Wiemann & Domke (1967): 285-346; Wiinstedt (1946): 313-316.

Gc Lichen steppe with *Corynephorus canescens* on dry dunes.

Dominant community - *Violo-Corynephorum* Westhoff (1943) 1947 (synon.: *Corynephorum maritimum* (Westhoff 1946) R.Tx. 1962).

Succession - The *Violo-Corynephorum* ("Silbergrasflur") occurs on almost decalcified dry dunes (0.3-0.004% lime and pH 5.8-4.4; Westhoff, 1947) and succeeds the *Elymo-Ammophiletum* (Aa), *Hippophaë* scrub (Bh) or dune grasslands (Gk). *Corynephorus canescens* also occurs as a pioneer on wandering dunes.

The lichen cover is very easily disturbed (e.g. by trampling). Westhoff (1947) describes a cyclic sere on the westerly West-Frisian islands: covering of lichens leads to erosion by wind, after which the pioneer phase of the *Violo-Corynephorum* occurs anew; succession to *Calluna* heath (Hc) also leads to domination by lichens and regression to a *Corynephorus* dune.

Succession to *Empetrum* heath (He) occurs mainly in the North-Frisian dune areas, stimulated by a light overblowing of sand (Heykena, 1965).

Distribution - The *Violo-Corynephorum* occurs as a stable terminal stage on many decalcified dunes, often on S- and W-exposures. On Sylt it mainly occurs in a narrow zone between the *Ammophila* dunes (Aa) and *Empetrum* heaths (He).

References - Boerboom (1960): 32-36; Heykena (1965): 40, 41, 59-62, 108, 109; Runge (1973): 41; Westhoff (1947): 87-91; Westhoff & Den Held (1969): 154, 155.

Gi Dwarf shrub vegetation with *Salix arenaria* on dry dunes.

Dominant communities - *Polypodio-Salicetum* (R.Tx. 1955 n.n.) Boerboom 1960, *Thalictro-Salicetum* R.Tx. 1937.

Succession - *Salix* shrubs ("Dünenweiden-Busch") in dry dunes are dependent on vegetative spreading. From moist slacks they can extend into dry *Hippophaë* scrub (Bh), dune grasslands (Gk) and *Corynephorus* dunes (Gc) (Boerboom, 1960). *Salix arenaria* also occurs as a pioneer with strong overblowing of sand (Heykena, 1965; Linke, 1960).

Distribution - On Rømø, the East- and West-Frisian islands, mainly on N-exposures and flat dune areas. On Sylt and Amrum on wandering dunes.

References - Boerboom (1960): 59-63; Doing (1974): 65-67; Heykena (1965): 53; Linke (1960): 407-416; Runge (1973): 222, 223; Sloet van Oldruitenborgh (1976): 72; Westhoff & Den Held (1969): 245, 246; Wiinstedt (1946): 315.

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Gr Dwarf shrub vegetation with *Rosa pimpinellifolia* on dry dunes.

Dominant communities - *Thalictro-Salicetum* R.Tx. 1937 (synon.: *Rosa spinosissima-Salictum arenaria* R.Tx. 1952), *Tortulo-Phleetum arenarii* (Massart 1908) Br.-Bl. et De Leeuw 1936, *Festuco-Galietum maritimi* (Onno 1933) Br.-Bl. et De Leeuw 1936.

Succession - On slightly calcareous dunes on Texel *Rosa pimpinellifolia* ("Dünenrosen-Gestrüpp") dominates the dune grasslands. Elsewhere *Rosa* shrub occurs locally on S-exposures in dune grasslands. This is a relatively late stage of succession.

Further succession to *Calluna* heath (Hc) occurs on Rømø, Sylt, Nordney (Heykena, 1965) and Texel as an effect of acidification of the top soil.

Distribution - Commonly occurring on Texel; locally on Rømø, Sylt, the East-Frisian islands, Ameland and Terschelling.

References - Boerboom (1960): 36; Heykena (1965): 58, 71, 106, 107, 121; Runge (1973): 221; Westhoff (1947): 78, 79, 81, 85; Westhoff & Den Held (1969): 156, 157, 245, 246; Wiinstedt (1946): 315, 319.

DUNE-HEATH LANDSCAPE ("Schwarzdünen", "duinheiden")

He Heath with *Empetrum nigrum* on dry and moist decalcified dune areas.

Dominant community - *Carici arenariae-Empetretum* R.Tx. et Kawamura 1975 (synon.: *Polypodio-Empetretum* (Meltzer 1941) Westhoff 1947, *Saliceto repentis-Empetretum* R.Tx. 1955 n.n., *Empetro-Genistetum tinctoriae* Westhoff (1947) 1968).

Succession - In stabilized decalcified dune areas (pH 5.0 - 4.1 resp. 4.4 - 3.7; Westhoff, 1947 resp. Heykena, 1965) *Empetrum* heath ("Krähenbeer-Heide") often occurs on somewhat moist N-exposures, succeeding Aa, Bh or Gk. On the dry S- and W-exposures there are dune grasslands (Gk, Gr) or lichen steppes with *Corynephorus* (Gc).

Most North-Frisian dune ridges lie perpendicular to the main direction of the wind and are therefore exposed to wandering sand. *Empetrum* heath is stimulated by a light overblowing of sand and under those circumstances it occupies all exposures in the decalcified dune area, succeeding the *Elymo-Ammophiletum* (aa) or the *Violo-Corynephorum* (Gc) (Heykena, 1965).

Stabilized older *Empetrum*-heaths in North-Friesland, Denmark and on Borkum are succeeded by *Calluna* heath (Hc), also on N-exposures (Heykena, 1965). Westhoff (1947) considers *Empetrum* heath on N- and E-exposures as a terminal stage.

Distribution - On decalcified acid dunes: a. on N-exposures (old dunes

in the entire area); b. with light overblowing of sand on all exposures of dry dunes (Sylt, Amrum, Eiderstedt); and c. in dry to moist slacks and flat areas (Danish and North-Frisian dune areas, Norderney, Terschelling, Vlieland, Texel).

References - Doing (1974): 65-67; Heykena (1965): 42-50, 56-59, 79-81, 83-86, 94, 95, 107-113, 121; Raabe (1964b): 169-175; Runge (1973): 189, 190; De Smidt (1977): 259-263; Tüxen & Kawamura (1975): 89-92; Westhoff (1947): 93-96, 116-119; Westhoff & Den Held (1969): 225, 226.

Hc Heath with *Calluna vulgaris* and *Empetrum nigrum* on dry and moist decalcified dune areas.

Dominant community - Carici arenariae-Empetretum R.Tx. et Kawamura 1975 (synon.: Empetro-Genistetum tinctoriae Westhoff (1947) 1968).

Succession - *Calluna* heath occurs in (flat) dune areas with a decalcified acid soil rich in humus (pH 3.9 - 3.4, humus content 8 - 10%; Heykena, 1965). In older stabilized dune areas it succeeds *Empetrum* heath (He), the Violo-Coryneporetum (Gc) and dune grasslands (Gk, Gr). *Calluna* decreases with grazing, manuring or overblowing by sand (Heykena, 1965), but may reestablish after stopping of these influences.

Raabe (1964b) considers *Calluna* heath as a natural terminal stage in the dune areas around the North Sea, Heykena (1965) does the same for the Danish and German dune areas. According to Westhoff (1947), however, *Calluna* heath on dry dunes is succeeded by the Violo-Coryneporetum (Gc) and on moist dunes by *Empetrum* heath (He) or brushwood (*Quercus roboris*-Betuletum; Wb). Only by regular management measures the *Calluna* heath may be maintained (Westhoff, 1947).

Distribution - In the decalcified Danish and North-Frisian dune areas *Calluna* heath occurs as the terminal stage of vegetation development, abundantly on Fanø and Rømø. On Amrum almost all dune heaths have been planted with coniferous forests (Raabe, 1963, 1964a).

In the East- and West-Frisian dune areas, which were decalcified more slowly, *Calluna* heath occurs locally on Wangerooge, Borkum, Ameland, Terschelling and Vlieland. It is common in old dune areas of SW-Texel.

References - Heykena (1965): 49, 50, 59, 68, 71, 79-81, 83-86, 94, 95, 108-113, 121; Raabe (1964b): 169-175; De Smidt (1977): 259-263; Tüxen & Kawamura (1975): 89-92; Westhoff (1947): 116-119; Westhoff & Den Held (1969): 225, 226; Wiinstedt (1946): 314, 315.

Hx Heath with *Carex nigra*, *Oxycoccus macrocarpos* and *Erica tetralix* in moist to wet acid dune slacks.

Dominant communities - Caricetum trinervi-nigrae Westhoff 1947, Cirsio-Molinietum Siss. et De Vries 1942, Nardo-Gentianetum pneumonanthes

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Preising 1950 em. Westhoff, *Empetro-Ericetum* Westhoff (1943) 1947 (synon.: *Saliceto arenariae-Ericetum tetralicis* R.Tx. et Buchwald 1942).

Succession - In the decalcified acid Danish and North-Frisian dune slacks (pH 4.7 - 3.9; Heykena, 1965) mainly the communities mentioned here ("nasse Heide") occur. Species of the *Caricetum trinervi-nigrae* ("Kriechweiden-Braunseggen-Sumpf") can pioneer on the bare sand. Acidification of brackish marshes (To; pH at Tipperne 6.1 - 4.9) may also lead to the *Caricetum trinervi-nigrae* (Gravesen, 1972).

Acidification of the calcareous dune slacks of the West- and East-Frisian islands leads from *Schoenus* marsh (Ws) via the *Caricetum trinervi-nigrae* (pH 5.9 - 4.5; Westhoff, 1947) to the *Cirsio-Molinietum*, the *Empetro-Ericetum* (pH 5.4 - 3.9; Westhoff, 1947) or to several brushwood communities (Wb).

Distribution - In the Danish and North-Frisian dune slacks and on older parts of beach plains. Locally in East- and West-Frisian dune slacks, mainly on Norderney, Terschelling, Vlieland and Texel.

References - Heykena (1965): 72-75, 86-90, 94, 95, 112, 123; Runge (1973): 175, 184; De Smidt (1977): 260, 263; Westhoff (1947): 109-116; Westhoff & Den Held (1969): 184, 185, 200, 216, 221, 222; Wiinstedt (1946): 316-318.

DUNE-SLACK - AND REED-MARSH LANDSCAPE ("Dünentäler", "Röhrichte"; "duinvalleien", "rietvelden")

Wp Reed marshes with *Phragmites australis* and *Scirpus maritimus* in wet dune slacks, on desalinating ungrazed beach plains and salt marshes and on brackish to fresh mud flats.

Dominant communities - Halo-Scirpion (Dahl et Hadac 1941) Westhoff & Den Held 1969, Phragmition (communis) W. Koch 1926 em. Balátová-Tulácková 1963.

Succession and distribution - In this specific legend unit reed marshes that developed in three different landscape types have been assembled:

- a. Occurring on wet (sometimes brackish) places in dune slacks (W) and in dune heaths (H) in the entire area; it can succeed the *Samolo-Littorelletum* Westhoff 1947, or extend into open water of dune lakes (Juist, Ameland, Texel).
- b. On places where fresh water seeps from bordering dune or Pleistocene areas and on the highest marshes in estuaries; absence of grazing on brackish marshes (T1, To) leads to reed marshes ("Röhrichte"), mainly on Skallingen, Fanø, Rømø, Sylt, Amrum and Eiderstedt and near Schönbüll, Arensch and Nieuw Statenzijl (Dollard).
- c. In the brackish and tidal freshwater parts in estuaries reed marsh-

es pioneer on mud flats. In a riverward direction at first *Scirpus maritimus* ("Brack-Röhricht") occurs and then, with a further decrease of salinity, *Phragmites australis* appears. These communities occur mainly in the estuaries of the rivers Ems (Dollard included), Weser, Elbe, Eider and Varde Aa and near sluices (Brede Aa, Vidaa). After silting up to a level over mean high water and with grazing the *Agrostis stolonifera salina*-sociation (Sf) develops.

References - Beeftink (1965): 123-126; Boerboom (1960): 50, 51; Fresco (1966): 14-16; Mikkelsen (1949): 304-307; Runge (1973): 112; Westhoff (1947): 105, 106; Westhoff & Den Held (1969): 134, 135, 176, 177; Wiinstedt (1946): 316, 317, 323.

Ws Marsh communities with *Schoenus nigricans*, *Salix arenaria* and *Calamagrostis epigejos* on desalinating beach plains and in moist calcareous dune slacks.

Dominant communities - *Junco baltici*-*Schoenetum nigricantis* (Westhoff 1943) Westhoff et Den Held 1969 (synon.: *Salici repentis*-*Schoenetum nigricantis* R.Tx. 1942), *Ophioglosso*-*Calamagrostietum epigeji* Westhoff et Segal 1961.

Succession - *Schoenus* marsh ("Kriechweiden-Schwarzried-Sumpf") can succeed several communities of the brackish zone (Tu, To). Soil acidity is 7.9 - 5.8 pH, lime content 0.3 - 0% (Heykena, 1965).

In older decalcified dune slacks *Schoenus* marsh is succeeded by the *Ophioglosso*-*Calamagrostietum*, the *Pyrolo*-*Salicetum* (Meltzer 1941) Westhoff 1947 (Ws/Hx) or the *Caricetum trinervi-nigrae* (Hx).

Distribution - Young calcareous dune slacks and desalinating beach plains on the West- and East-Frisian islands.

In the North-Frisian and Danish dune areas the acidity of the decalcified soil is too high to allow for any *Schoenus* marsh development.

References - Doing (1974): 60-62, 66; Heykena (1965): 110-112; Runge (1973): 180; Westhoff (1947): 106-109, 111-113; Westhoff & Den Held (1969): 205, 206, 226, 227; Wiinstedt (1946): 317.

Wb Brushwood with *Betula pubescens* (*Myrica gale* and *Alnus glutinosa*) in moist dune slacks.

Dominant communities - *Quercus roboris*-*Betuletum* R.Tx. (1930) 1937, *Myricetum gale* (Gadeceau 1909) Jonas 1935, *Frangulo*-*Salicetum auritae* (Malcuit 1929) Doing 1962 em. Westhoff, *Alno*-*Salicetum cinereae* (Al-lorge 1922) Doing 1962 em. Westhoff, *Salicetum pentandro-arenariae* Westhoff (1968 n.n.) Westhoff et Den Held 1969).

Succession - *Myrica*, *Salix* and *Betula* brushwoods appear in wet heaths

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(Hx), *Betula* brushwood also occurs in drier *Calluna* and *Empetrum* heaths (Hc, He).

Investigators do not agree on the point of woodland formation. Westhoff (1961) considers (brush-)wood as a natural terminal stage in moist dune slacks of the West-Frisian islands. According to Ellenberg (1963) all dune areas of the North Sea islands can develop to woodland, starting from the slacks, in spite of the strong winds. Raabe (1964b), on the contrary, considers *Calluna* heath as the natural terminal stage in the dune areas around the North Sea, Heykena (1965) does the same for the Danish and German dune areas and so does Klement (1953) for the East-Frisian dune areas. According to Doing (in chapter 6.2) soil fertility is a vital factor for the development of woody species under the climatic conditions of the Wadden Sea islands.

Distribution - On the West- and East-Frisian islands a natural development to woodland takes place only in sheltered moist slacks, not on dry dunes; mainly on Texel, Vlieland, Terschelling, Schiermonnikoog, Borkum (planted) and Norderney.

The Schwimmendes Moor, occurring outside the dikes in the Jadebusen, consists of a living peatmoor (H) upon which since the twenties brushwood develops (Wiermann, 1965).

In the North-Frisian and Danish dune areas there is no naturally developed woodland, except for a small *Salix* scrub on Rømø near Lakkolk.

References - Doing (1962): 65-71; Heykena (1965): 112; Runge (1973): 202, 204, 218; Westhoff (1947): 111, 116, 118, 119; Westhoff & Den Held (1969): 232-235, 258, 259; Wiinstedt (1946): 318.

BRACKISH TRANSITION LANDSCAPE ("Übergangszonen Salz-Süss", "zout-zoet overgang")

Carpets of dwarf plants with *Sagina maritima*, *Cochlearia danica* and *Sagina nodosa* intermingling other communities in these zone.

Communities - *Sagina maritima*-*Cochlearia danica* (R.Tx. 1937) R. Tx. et Gillner 1957, *Centaureo-Saginetum moniliformis* Diemont, Siss. et Westhoff 1940 (synon.: *Gentiano uliginosa*-*Centaureietum vulgare* Br.-Bl. et De Leeuw 1936), *Cicendietum filiformis* Allorge 1922.

References - Beeftink (1965): 126-128; Dijkema (1975): 30; Doing (1974): 56, 57; Runge (1973): 46, 47, 125, 126; Westhoff (1947): 100-102; Westhoff & Den Held (1969): 74-76, 113, 166, 167.

Tu Open communities with *Spergularia marina*, *Glaux maritima*, *Agrostis stolonifera* and *Juncus anceps* on beach plains and in young dune slacks.

Dominant communities - *Glaux maritima*-society Beeftink 1962, *Puccinellietum distantis* Feekes (1934) 1943, *Puccinellietum retroflexae*

(Almquist 1929) Beeftink 1965, Parnassio-Juncetum atricapilli (Westhoff 1947) Westhoff et Den Held 1969.

Succession - On beach plains and in young dune slacks dependent on salinity, moisture and washing or blowing of sand several pioneer communities are possible. Succession leads to brackish grassland (To) or *Schoenus* marsh (Ws).

In the decalcified acid Danish and North-Frisian dune slacks species of the Caricetum trinervi-nigrae (Hx) often occur as pioneers.

Distribution - On the West- and East-Frisian islands; locally on North-Frisian and Danish beach plains. The distribution of the Puccinellietum retroflexae is not well known and very scattered.

References - Beeftink (1965): 115-120, 122, Runge (1973): 123, 124; Westhoff (1947): 98, 99, 123-125; Westhoff & Den Held (1969): 174-176, 204, 205.

To Closed grasslands with *Ononis spinosa*, *Lotus corniculatus*, *Agrostis stolonifera*, *Carex distans*, *Juncus maritimus* and *Blysmus rufus* on transitions between salt marshes or beach plains and young dune slacks or dunes.

Dominant communities - Community of *Ononis spinosa* and *Carex distans* Runge 1966 pro ass. (synon.: Ononido-Caricetum distantis R.Tx. 1955 n.n.), Community of *Agrostis stolonifera* subvar. *salina* and *Trifolium fragiferum* Westhoff 1947, *Juncus maritimus*-*Oenanthe lachenalii* association R.Tx. 1937 (synon.: Juncetum maritimi Blik 1956), Junco-Caricetum extensae blysmetosum rufi Westhoff 1947, Scirpetum rufi (G.E. et G. Du Rietz 1925) Gillner 1960.

Succession - On dry sandy beach plains and salt marshes the Community of *Ononis spinosa* and *Carex distans* ("Hauhechel-Lückenseggen-Rasen") occurs on the transition of salt marsh (Sf) and dry dunes (A, B, G). Without grazing a vegetation of tall herbs dominated by *Elymus pycnanthus* (= *Agropyron pungens*) may develop.

The other communities in these brackish zones occur on moist sandy soils; they succeed the *Armerion maritimae* (Sf). On calcareous soil further succession leads to *Schoenus* marsh (Ws) and on a decalcified acid soil it leads to wet heath communities (Hx).

With a sufficient fresh water supply lack of grazing may lead to reed marsh (Wp).

Distribution - Mainly on Skallingen, Mandø, Fanø, Rømø, Eiderstedt near St. Peter, the East- and West-Frisian islands. Extensive green beaches with well developed transition communities are restricted to Texel (Slufter), Eiderstedt (St. Peter-Böhl) and Rømø (entire west-coast).

In the North-Frisian and Danish area marshes with *Juncus maritimus* ("Meerbinsen-Ried") are rare due to edaphic factors, except for the vi-

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cinity of St. Peter (Raabe, 1970).

References - Beeftink (1965): 111-113; Doing (1974): 56-58; Menke (1969): 100-107; Mikkelsen (1949): 297; Runge (1973): 125, 126; Westhoff (1947): 127-131; Westhoff & Den Held (1969): 110, 113, 123, 173, 174; Wiinstedt (1946): 311, 313, 314, 323.

T1 Brackish pastures with *Lolium perenne*, *Trifolium repens* and *Elymus* (= *Agropyron*) *repens* on the highest (grazed) salt marshes, often protected by a low summer-dike.

Dominant communities - *Agropyretum repentis maritimum* Nordh. 1940, *Poo-Lolietum* D.M. de Vries et Westhoff n.n. apud A. Bakker 1965, *Potentillo-Festucetum arundinaceae* Nordh. 1940.

Succession - On the highest clayish salt marshes and in summer-polders in the storm flood zone naturally developed pastures occur. The *Poo-Lolietum* is comparable with intensively cultivated inland pastures. With decreasing salinity these brackish pastures ("alte Hellerweiden") succeed the *Armerion maritimae* (Sf).

When there is a sufficient supply of fresh water absence of grazing may lead to reed marshes (Wp).

Distribution - The *Poo-Lolietum* is not found on Danish salt marshes. For the rest the *Agropyretum repentis maritimum* and the *Poo-Lolietum* are common on the oldest salt marshes and in summer-polders (mainly the Ho Bugt, the Danish coast between St. Darum and Ballum, the coast between Cuxhaven and the Weser, the East-Frisian coast, the Dutch Groningen and Frisian coast), in estuaries (Varde Aa, Elbe, Weser, Dollard), on some "Halligen" (Hooge, Oland, Langeness) and on some intensively grazed island marshes (Fanø, Rømø, Langeoog, Ameland). The *Potentillo-Festucetum arundinaceae* mainly occurs in estuaries.

In consequence of strengthening of dikes in recent years many marshes of this type have been lost by embankment (Højer, Hauke Haien-Koog, Norderfriedrichskoog, North-Dithmarschen, Meldorfer Bucht, Elbe-estuary, between Minsen and Harlesiel, Westaccumersiel, Borkum, Lauwerszee).

References - Beeftink (1965: 139-141; Dijkema (1975): 30, 31; Doing (1974): 56-58; Fresco (1966): 21-26; Mikkelsen (1949): 297; Runge (1973): 129, 130; Westhoff & Den Held (1969): 107-111, 113, 114, 188, 189.

SALT-MARSH LANDSCAPE ("Salzmarsch-Rasen", "kwelders")

On marshes enriched with tidal drift material halo-nitrophilous communities develop with *Suaeda maritima*, *Atriplex hastata*, *Atriplex littoralis* and *Elymus pycnanthus* (= *Agropyron pungens*). Usually they form narrow zones and cannot be mapped.

Communities - Suaedetum maritimae (Conard 1935) Pignatti 1953, Atriplicetum littoralis (Warming 1906) Westhoff et Beeftink 1950, Atriplici-Agropyretum pungentis (Beeftink et Westhoff 1962).

References - Beeftink (1965): 130, 131, 133-135, 143, 144; Dijkema (1975): 24, 28; Runge (1973): 49, 80; Westhoff & Den Held (1969): 70, 71, 123.

Ss Halophytic pioneer communities with *Spartina anglica* and *Salicornia europaea* within daily tidal range and on beach plains.

Dominant communities - Spartinetum townsendii Corillon 1953, Thero-Salicornion Br.-Bl. 1933 em. R.Tx. 1950.

Succession - On the highest parts of the tidal flats *Spartina anglica* ("Schlickgras-Gesellschaft") and *Salicornia europaea* ("Queller-Gesellschaft") are the first vascular plants escorting salt marsh development. The perennial *Spartina* occurs on a soil rich in water and clay, the annual *Salicornia* on more drained places (and also on lower parts of beach plains). After silting up to the level of mean high water the Puccinellietum maritimae (Sp) takes over.

In order to promote land reclamation *Spartina anglica* was introduced in the entire Wadden Sea area in the ninetwenties (Van Eerde, 1942; Forschungsstelle Norderney, 1973; Jørgensen, 1934; Kamps, 1962; Kolombe, 1931; König, 1948; Meesenburg 1971; Pedersen, 1970). It is in competition with *Salicornia* and *Puccinellia* (Sp) and locally it may replace their zones completely. Usually however it is less successful: on the islands, because of the sandy character of the salt marshes; on the more clayish salt marshes along the mainland coast as a consequence of an artificial drainage system and of grazing.

Distribution - Widespread in the entire area, where the tidal flats of the Wadden Sea border on the salt marshes of the islands or mainland. Often too small for mapping. The pioneer communities are lacking at eroded salt marshes (cliff on the map). Locally found on beach plains e.g. on Spiekeroog and Schiermonnikoog. *Spartina*-swamps occur only locally, e.g. on Trischen.

References - Beeftink (1965): 87-89, 91-94; Dijkema (1975): 23, 24; Runge (1973): 47, 48; Tüxen (1974): 117-174; Westhoff (1947): 122; Westhoff & Den Held (1969): 68, 69, 99, 100; Wiinstedt (1946): 311, 323.

St Pioneer community with *Aster tripolium* on mud flats.

Dominant community - *Aster tripolium*-sociation Beeftink 1965.

Succession - The *Aster*-sociation occurs on estuarine marshes as a

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pioneer on soft mud flats rich in organic matter. The plants grow in a very optimal and vital way and may form stands of up to 250 cm in height.

Aster tripolium also develops (less optimally) on ungrazed *Puccinellia* marshes along the mainland; this vegetation is included among those of the *Puccinellia* zone (Sp).

Distribution - At present only known from one site: the SW part of the Dollard. In 1948 Linke described a comparable community from the Leybucht and the Jadebusen (Forschungsstelle Norderney, 1973).

References - Beeftink (1965): 120, 121; Fresco (1966): 13, 14.

Sp Halophytic grasslands and dwarf shrub vegetation with *Puccinellia maritima*, *Limonium vulgare* and *Halimione portulacoides* on low salt marshes and beach plains.

Dominant communities - *Puccinellietum maritimae* (Warming 1890) Christiansen 1927, *Plantagini-Limonietum* Westhoff et Segal 1961, *Halimionetum portulacoidis* Kuhnholz-Lordat 1927.

Succession - After a tidal flat has silted up to the level of mean high water the colonists (Ss, St) are succeeded by the communities of the *Puccinellion maritimae* ("Andelzone"). *Puccinellia maritima* is the most successful species in salt marsh development and tillers rapidly. *Puccinellia* grasslands are favoured by grazing.

On naturally developed salt marshes of the islands and "Halligen" on this level the formation of creek banks and basins begins. *Limonium vulgare* may dominate beach plains and badly drained back-swamps. The conspicuous species occurs in a variant of the *Juncetum gerardii* (Sf) as well. The more clayish basins are dominated by *Spartina anglica*.

Halimione portulacoides, on the contrary, develops on well-drained creek levees, terraces and beach plains and on the equivalent sites in artificially drained and more clayish salt marshes along the mainland.

On sandy beach plains with a variable salinity a rather open *Puccinellia* grassland with e.g. *Parapholis strigosa*, *Elymus farctus* (= *Agropyron junceum*) and *Agrostis stolonifera* succeeds the thinly arranged *Salicornia* colonists (sand halosere).

Distribution - Grazed *Puccinellia* grasslands are widespread, especially along the mainland. *Limonium vulgare* occurs mainly on the islands (e.g. Skallingen, Oldsum-Föhr, Spiekeroog, Schiermonnikoog, Terschelling, Texel) and on the "Halligen" (Gröde, Nordstrandischmoor). The *Halimionetum* occurs abundantly on Skallingen, on some artificially drained salt marshes (e.g. northern coast of Groningen, Norderney, Tümlauer Bucht, Oland) and locally in the entire area, except for estuaries, e.g. near Oldsum-Föhr, on the Bosplaat of Terschelling, Rotumerplaat and De Schorren on Texel.

References - Beeftink (1965): 96-103; Dijkema (1975): 24-28; Heykena (1965): 25, 26; Mikkelsen (1949): 295, 296; Runge (1973): 122, 123; Westhoff (1947): 122, 123; Westhoff & Den Held (1969): 169-171; Wiinstedt (1946): 323.

Sf Halophytic grasslands with *Festuca rubra*, *Juncus gerardii* and *Agrostis stolonifera* on high salt marshes, brackish marshes and beach plains.

Dominant communities - Artemisietum maritimae (Hoquette 1927) Br.-Bl. et. De Leeuw 1936, Juncetum gerardii Warming 1906, Junco-Caricetum extensae pholiuretosome Westhoff 1947, *Agrostis stolonifera salina*-sociation Beeftink 1962.

Succession - With silting up of the salt marsh over the average spring-tide level communities of the *Armerion maritimae* ("Schwingelzone") takes over.

The Artemisietum succeeds the Halimionetum on creek levees and on the equivalent habitat of artificially drained salt marshes.

On the islands and "Halligen" the *Puccinellia* zone (Sp) is succeeded mainly by the Juncetum gerardii with *Armeria maritima* ("Grasnelken-Wiese") or with *Limonium vulgare* ("Strandflieder-Salzbinsen-Wiese"). On most sandy beach plains the Junco-Caricetum extensae occurs as a pioneer (Westhoff, 1947) or succeeds the Puccinellietum (sand halosere). Further silting-up, overblowing by sand or embankment by a low summer-dike leads to brackish grassland (mainly To).

On the clayish salt marshes along the mainland the *Puccinellia* zone is succeeded by *Festuca-Agrostis* (-*Juncus gerardii*) grasslands, which belong to the Juncetum gerardii too. Further silting up or embankment by a summer-dike leads to brackish pastures (T1).

In a landward direction in estuaries the species of the high salt marsh shift to a lower level within the zonation. Thus the *Agrostis*-sociation appears in the brackish part of estuaries from the mean high water level onwards. Further silting up leads to brackish pastures (T1).

Distribution - Grasslands with *Armeria* are common on the high salt marshes and beach plains of most dune islands, on the "Halligen", the Grüne Insel and Neuwerk. The Artemisietum maritimae is locally found in the entire area. Some artificially drained salt marshes (e.g. Norderney, Nessmersiel) are dominated by *Artemisia maritima*. *Festuca-Agrostis* grasslands occur along the mainland in the entire area. The Junco-Caricetum is common on beach plains of Skallingen and the East- and West-Frisian islands.

Brackish *Agrostis* grasslands occur near the Varde Aa, the Eider, along the north bank of the Elbe near Neufeld, in the Dollard and in the Hauke Haien-Koog.

References - Beeftink (1965): 103-112, 123; Dijkema (1975): 28-31; Fresco (1966): 19-21; Heykena (1965): 25, 26; Mikkelsen (1949): 296;

Runge (1973): 124, 127, 128; Westhoff (1947): 125-129; Westhoff & Den Held (1969): 171-174; Wiinstedt (1946): 323.

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