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Key environmental variables determining the occurrence and life span of basiphilous dune slack vegetation

E. J. LAMMERTS[1]* and A. P. GROOTJANS[2]

[1]*Ministry of Agriculture, Nature Management and Fisheries, PO Box 30027, 9700 RM Groningen, The Netherlands; and* [2]*Laboratory of Plant Ecology; University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*

SUMMARY

Environmental processes controlling the occurrence of basiphilous pioneer vegetation were identified in seven representative dune slacks on the Dutch Wadden Sea Islands. The variation in vegetation and relations with soil and groundwater composition were established first. Cluster analysis of the vegetation in the dune slacks resulted in six subtypes of basiphilous pioneer vegetation and three types representing older succession stages. Canonical correspondence analysis suggested that moisture and pH are the main habitat factors in the dataset and that habitats of older succession stages, compared to basiphilous pioneer stages, are either acidified or eutrophicated. A principal component analysis of shallow groundwater samples from all dune slacks revealed the dominant influence of inundation with sea water in the total dataset. In the freshwater dataset Ca^{2+} and HCO_3 concentrations predominated. Cl^- and Ca^{2+} concentrations of shallow groundwater were, therefore, considered key variables in describing the environmental processes determining suitable habitat conditions for basiphilous pioneer vegetation. To be able to distinguish between a conditioning role of the hydrological regime (c.q. exfiltration of mineral rich groundwater) and a conditioning role of (former) geomorphological processes (c.q. the presence of $CaCO_3$ minerals), the soil $CaCO_3$ content was added as key environmental variable. In primary dune slacks on the islands of Schiermonnikoog and Texel, having comparable initial lime contents (0.5–1%), the life span of basiphilous pioneer vegetation was estimated to be 30–50 years without a mowing regime and 100–150 years under a mowing regime. In secondary dune slacks the life span of basiphilous pioneer vegetation varies considerably with differences in local circumstances, especially in strength of prevailing pH-buffering mechanisms. These, in turn, are determined by differences in environmental conditions on a landscape scale (hydrology, geomorphological history).

Key-words: Caricion davallianae, decalcification, groundwater composition, hydrology, succession.

* Correspondence author.

Nomenclature follows Van der Meijden (1990) for phanerogams, Touw & Rubers (1989) for musci, Margadant & During (1982) for hepaticae and Schaminée *et al.* (1995) for syntaxa.

INTRODUCTION

A century ago most of the Dutch coastal dunes were dynamic: new dune slacks were formed by dune ridges enclosing parts of sandy beach plains (primary dune slacks) or by blow-outs in older dune areas (secondary dune slacks). A complete range of successional stages of dune slack vegetation was present at that time (Holkema 1870; Van Eeden 1886; Van Dieren 1934; Westhoff 1947). Nowadays the more mature stages (shrub and forest) prevail in wet dune slacks and the pioneer stages have become rare (Van Dorp *et al.* 1985). During the last 20–40 years the basiphilous pioneer community, in particular, with many rare and protected plant species, classified as *Caricion davallianae*, has decreased considerably in the Netherlands (Mennema *et al.* 1985; Grootjans *et al.* 1988), while acidophilous communities have increased. The terms 'acidophilous' and 'basidophilous' are used here to indicate preferences of plant species to certain pH ranges. The shift in species composition was partly due to natural succession but human activities such as drainage, afforestation and abstraction of drinking water have contributed significantly to the decline of basiphilous pioneer stages (Van Dijk & Grootjans 1993). Attempts have been made to stop this decline by executing restoration projects, usually sod cutting, which renew the succession.

Basiphilous pioneer communities in dune slacks are typically restricted to environments of a very low nutrient status, particularly regarding nitrogen and phosphorus (Willis 1963; Dougherty *et al.* 1990; Koerselman & Meuleman 1996; Lammerts & Grootjans 1997). The soil pH is buffered above 6·0 (Sival 1996). Under average climatological conditions the winter groundwater levels are slightly above the soil surface while the summer levels do not exceed *c.* 80 cm below the surface (Lammerts *et al.* 1995). The slacks are generally fed with fresh water, but inundation with salt water can occur in primary beach plains (Holkema 1870; Westhoff 1947; Lammerts *et al.* 1992).

This paper focuses on identifying key environmental variables which determine the occurrence of basiphilous dune slack vegetation. For planning purposes these variables should be easy to measure. In particular, they should also yield information on restoration perspectives. Therefore they are to describe mechanisms, such as pH-buffering and nutrient accumulation, rather than actual habitat conditions (soil acidity and nutrient status) which often are representative for local and transient circumstances only. Processes related to these mechanisms should also be considered, i.e. (de)-calcification, (de)salinization and groundwater discharge (Bakker 1990; Stuyfzand 1990, 1993; Lammerts *et al.* 1995). The perspectives for basiphilous pioneer vegetation will be depicted not only in terms of occurrence but also in terms of the life span that may be expected.

Two pH-buffering mechanisms are generally considered to be important in calcareous dune slacks: dissolution of calcite and exchange of Ca^{2+} and H^{+} ions on the soil exchange complex, both operating on the H_2CO_3–HCO_3^-–CO_2 equilibria (Bruggenwert *et al.* 1991; Sival 1996). On a landscape level these buffer mechanisms are supported by:

(1) Periodic inundation with brackish water, which is a mixture of salt water and precipitation water; this process leads to buffering by the soil exchange complex.
(2) Geomorphological processes producing calcareous pioneer habitats; wind blowing may in dune slacks cause a removal of decalcified sand or a supply with calcareous sand, developing dune ridges may enclose new dune slacks on calcareous beach

plains; these processes lead to pH-buffering by dissolution of calcite in the rooting zone (Rozema *et al.* 1985; Stuyfzand 1993; Sival 1996).

(3) Exfiltration of calcareous groundwater in decalcified slacks as a result of groundwater flow from surrounding dune areas (Bakker & Nienhuis 1990); sometimes precipitation of secondary $CaCO_3$ may occur when groundwater is saturated with respect to calcite (Sival *et al.* 1997); these processes lead to pH-buffering by the soil exchange complex, sometimes in combination with dissolution of $CaCO_3$.

The nutrient conditions needed for dune slack plants are difficult to assess. The total pool of nutrients does not necessarily reflect the nutrient status of a habitat (Wheeler & Shaw 1995). The availability of phosphorus may not be related at all to the total amount of phosphorus in the soil, since considerable amounts of mineral P may be chemically bound in calcareous soils and are often unavailable for plant growth (Rorison 1960; Etherington 1982). However, Olff *et al.* (1993), working in a coastal beach plain, found that, except for very young successional stages, the amount of mineralized nitrogen in the vegetation period was correlated with the total amount of organic matter in the topsoil. Lammerts & Grootjans (1997), reviewing studies on nutrient limitation in calcareous dune slacks, concluded that practically all cases studied pointed to nitrogen limitation, sometimes in combination with phosphorus limitation (cf. Van Beckhoven 1995; Koerselman & Meuleman 1996). The total amount of organic matter may, therefore, be a good indicator of nutrient status in dune slacks. The same applies to the accumulation speed of organic matter as an indicator of the rate of nutrient accumulation and of the expected life span of pioneer vegetation.

In the present study the vegetation descriptions and associated hydrochemical and soil data were derived from transects in seven representative dune slacks from five Wadden Sea Islands. Our questions regarding this dataset are: (i) which abiotic factors, measured in the topsoil (i.e. on the level of the habitat), explain most of the variation in species composition and how are these factors related to the occurrence of basiphilous pioneer vegetation, (ii) which environmental variables should be measured to evaluate the prospects for successful restoration of the habitats of this vegetation, once disappeared, and (iii) which is the life span of basiphilous pioneer vegetation to be expected in different dune slacks?

STUDY AREA

The study area consists of seven dune slacks (Fig. 1) comprising different stages in vegetation succession. The selected dune slacks are representative for most of the variation in dune slack types on the Dutch Wadden Sea Islands.

Primary dune slacks

The Strandvlakte is a young (*c.* 30 years) beach plain in the north-eastern part of Schiermonnikoog. Salt water can flood the plain only at very high tides. A threshold prevents rapid retreat of the surface water, which is diluted with precipitation water during the wet season. The water table drops below the surface in late spring due to evaporation and infiltration (Olff *et al.* 1993). The soil is still calcareous (*c.* 1·5% $CaCO_3$; Van Oosten 1986). From east to west a vegetation gradient can be seen where a salt marsh vegetation gradually changes into a well-developed *Junco baltici–Schoenetum* vegetation, with brackish *Scirpus maritimus*/*Phragmites* vegetation as an intermediate.

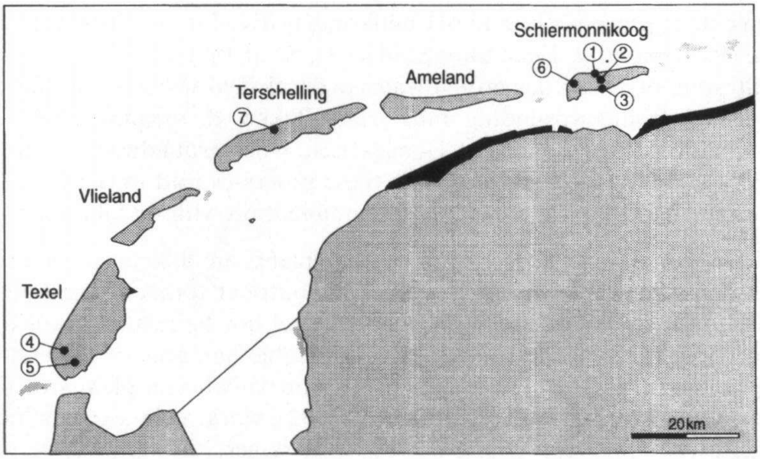

Fig. 1. The locations of the investigated sites on the Dutch Wadden Sea Islands. 1. Strandvlakte, 2. Bernhardweg valley, 3. Griënglop, 4. Moksloot valley, 5. Looodsmansduin valley, 6. Vuurtoren valley, 7. Koegelwieck.

The transect studied was situated in the *Schoenetum* community perpendicular to the dune ridge.

The Bernhardweg valley is located behind the Strandvlakte but is much older (*c.* 100 years). Inundation with salt water occurs though with low frequency. The topsoil is decalcified only in the most western part of the slack. A *Caricetum nigrae* community with many basiphilous species such as *Pedicularis palustris*, *Dactylorhiza incarnata* and *Epipactis palustris* is found here. This vegetation is mown almost every year. Data from a transect in this part of the slack are used.

The Griënglop is an old primary dune slack (*c.* 400 years old) at the south-eastern inner dune fringe of Schiermonnikoog, adjacent to the drained polder area. The soil is completely desalinated. In the past the aforementioned basiphilous species were present in large numbers. The slack has long been decalcified and is nowadays characterized by vegetation belonging to *Caricetum trinervi-nigrae*, *Violion caninae* and, locally, *Junco–Molinion*. There is only a thin organic top layer (not more than *c.* 5 cm). The Griënglop has been used by agriculture since 1925: as arable land and for sod cutting, haymaking and grazing. The management at present is mowing and grazing. The transect represents the central part of the slack.

The Moksloot valley at the southern part of the island of Texel is *c.* 200 years old. One hundred years ago a new dune ridge was formed along the coast. As a consequence the groundwater table has risen considerably. The slack had extensive mesotrophic marshes at that time (Holkema 1870). Afterwards a retreat of the west coast (leading to a decrease of the freshwater body which causes a lowering of the average groundwater level), the digging of a ditch (the Moksloot) in 1880, deep drainage in the adjacent polder area and abstraction of groundwater for drinking water purposes (since 1956) have led to much drier conditions. In 1991 eutrophic *Phragmition* and *Magnocaricion* marshes dominated the lower part of the slack. The higher parts were mown every year and consisted of a species-rich grassland (*Violion caninae*). The transect studied covered this gradient.

Secondary (sand-blown) dune slacks

The Loodsmansduin valley is a very small dune slack (*c.* 1200 m^2) at the eastern fringe of the Moksloot valley. At the eastern side it is bordered by a dune massif. The slack is over 200 years old. Since 1982 a basiphilous pioneer vegetation with *Schoenus nigricans* has established due to mowing. Data from an east–west orientated transect are used.

The Vuurtoren valley on Schiermonnikoog is also a small dune slack (*c.* 2500 m^2). The slack was colonized by pioneer vegetation about 40 years ago. It is situated in a dune area with a complex history which is mirrored by a varied lime content and vegetation. A well-developed *Schoenetum* vegetation in mosaic with *Pyrolo–Salicetum* is present. Scrub vegetation (*Hippophaë rhamnoides*) is expanding locally, especially on the slopes. The transect comprises a gradient from a slope into the slack.

The Koegelwieck is the largest secondary dune slack (*c.* 50 ha) on the island of Terschelling. It had been formed between 1825 and 1885 (van Dieren 1934). The development of the present vegetation started a few years after the last of some sea intrusions (*c.* 1920). Large sod-cutting experiments were carried out in this slack in 1956, 1959, 1986 and 1990. The actual spatial patterns resulting from these experiments, together with older data on vegetation composition (Mörzer Bruijns 1951; Westhoff & Van Oosten 1991), can be used for the reconstruction of time series. *Centaurio–Saginetum moniliformis* and *Samolo–Littorelletum* appear to be the dominant pioneer communities in the Koegelwieck. After 3–4 years they are succeeded by *Caricion davallianae* vegetation which, after a relatively short period (10–20 years), transgredes into stands dominated by *Calamagrostis epigejos*, *Salix repens* and *Oxycoccus macrocarpos*. In the oldest parts a tall *Calamagrostis epigejos–Ophioglossum vulgatum* frame community is present. From the actual chronosequence, as well as from historical descriptions, we can deduce that pioneer vegetation changes into *Calamagrostis* and *Salix* stands within 30–40 years. The transect studied passes through all stages of the chronosequence.

METHODS

Vegetation

One hundred and nine relevés of $2 \times 2\,m^2$ were recorded between 1987 and 1991 using a refined Braun–Blanquet cover–abundance scale (Londo 1976).

Soil

In July and August of 1991 soil samples were taken in triplicate within 1 m of the vegetation relevés in the organic top layer (0–10 cm) and in the mineral layer immediately below this layer (usually 10–20 cm below the surface). Duplicate soil samples were taken at the filter depths of the groundwater tubes (see below). PH(H_2O), pH(KCl), $CaCO_3$% (extraction with 0·1 n HCl) and % organic material (by loss of ignition at 500°C) were measured. NaCl was determined in a 1:8 soil:water solution, total nitrogen by digestion with phenol-H_2SO_4 + Se and colorimetric analysis of NH_3 using endophenol blue with salicylate, total phosphorus by digestion with $H_2SO_4 + HNO_3$ and colorimetric analysis of PO_4^{3-} using ammonium molybdate, and total carbon by a Carmhomat analyser with correction for $CaCO_3$.

Table 1. Vegetation types belonging to the association *Junco baltici–Schoenetum nigricantis*. Based on vegetation data from the Dutch Wadden Sea Islands, analysed with the clustering program *vg-aclus* from the program package VEGROW (Fresco 1991)

	Ia														Ib							
	221	222	246	208	224	225	226	251	227	228	206	207	220	205	237	249	244	232	253	241	255	256
Armerion maritimae																						
Scirpus maritimus	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–
Glaux maritima	1	1	–	–	1	–	1	1	1	–	–	1	1	–	–	–	–	–	–	–	–	1
Juncus maritimus	–	1	3	–	–	–	1	2	1	–	–	1	–	10	12	–	–	–	–	–	–	1
Carex distans	–	–	1	–	–	1	3	8	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Juncus gerardii	12	40	5	–	–	20	20	3	30	30	–	–	3	3	1	1	3	1	12	20	5	8
Festuca rubra	5	1	–	1	–	1	–	5	–	3	–	1	1	50	–	–	–	–	1	–	–	–
Samolo–Littorelletum																						
Samolus valerandi	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Littorella uniflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nanocyperion flavesc.																						
Linum catharticum	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Radiola linoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Carex oederi	3	1	–	–	–	1	1	1	–	–	–	–	1	–	5	5	5	3	1	3	1	1
Leontodon saxatilis	5	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–
Sagina procumbens	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Pellia epiphylla	20	–	–	5	–	1	1	–	1	–	–	10	1	1	–	–	–	–	–	–	–	–
Junco baltici–Schoenetum nigricantis																						
Schoenus nigricans	40	1	20	40	1	5	20	12	3	1	10	40	40	2	5	3	–	–	–	–	1	–
Parnassia palustris	1	–	–	1	–	1	1	1	–	1	1	1	1	–	–	–	–	–	–	–	–	–
Liparis loeselii	1	–	–	1	–	–	–	1	–	–	1	1	1	1	–	–	–	–	–	–	–	–
Eleocharis quinqueflora	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	1	–	–	1
Dactylorhiza incarnata	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	–	–	–	–	–	–
Carex flacca	12	–	1	1	–	1	1	3	–	–	1	1	7	1	1	3	–	–	–	1	–	1
Juncus subnodulosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Juncus aplinoarticulatus	12	1	3	1	1	–	3	1	1	–	–	1	3	1	3	5	–	1	1	1	1	1
Epipactis palustris	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	1	–	–	1	–	–	–
Equisetum variegatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pediculularis palustris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calliergonella cuspidata	–	–	–	50	–	–	–	–	–	40	20	30	–	–	–	8	12	1	8	30	47	1
Campylium sp.	30	5	1	–	5	1	1	1	1	–	–	–	3	–	1	–	–	–	1	1	12	1
Campylium stellatum	–	–	–	10	–	–	–	–	–	–	30	1	–	1	–	–	–	–	–	–	–	–
Drepanocladus aduncus	1	1	–	–	–	1	1	1	–	–	–	–	3	–	–	–	–	–	1	1	5	–
Pyrolo–Salicetum																						
Pyrola rotundifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gymnadenia conopsea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fissidens adianthoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Frame community of:																						
Calamagrostis epigejos	–	–	–	5	–	30	–	–	–	–	10	1	–	1	–	8	–	–	–	1	3	–
Ophioglossum vulgatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lolio–Potentillion																						
Agrostis stolonifera	–	1	1	1	1	–	1	3	1	1	3	3	1	3	–	–	–	–	–	1	–	–
Eleocharis pal., ssp. *unigl.*	–	–	–	–	1	–	–	–	–	–	–	–	–	1	1	–	3	1	–	3	1	3
Hydrocotyle vulgaris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	12	12	1	1	–	1	8
Potentilla anserina	1	30	20	1	20	1	3	8	20	8	–	1	1	5	1	8	12	1	1	3	5	12
Juncus articulatus	5	1	–	–	–	–	1	–	1	1	–	–	7	–	1	1	–	1	1	1	–	1
Trifolium repens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–

Ic					Id										Ie								If					
146	150	151	147	145	181	172	176	177	185	186	187	178	173	171	110	111	112	113	114	115	116	117	210	233	238	219	248	229
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	3	1	–	–	–	–	–	1	1	1	1	1
–	–	–	–	–	–	1	5	1	5	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	10	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	10	10	1	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	1	–
–	–	–	–	–	1	3	–	–	1	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	1	–	–	3	3	5	7	1	–	3	1	12	1	3	–	–	–	–	–	–	–	–	–	–	–	–	–	1
–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
30	10	10	30	40	10	5	–	20	1	3	2	3	12	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–
–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	1	3	1	1	–	–	–	–	–	–	–	–	20	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
1	10	10	1	3	1	1	1	–	–	1	1	1	1	–	1	1	1	1	1	1	1	1	–	1	1	–	5	1
5	1	1	3	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	5	1	1	3	3	3	5	1	3	1	–	–	–	–	–	–	–	–	–	1	–	–	1	1.
–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	5	5	3	3	5	5	5	5	3	–	–	–	–	1
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	1	1	1	1	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	5	12	2	–	1
30	–	–	–	60	–	–	–	–	1	10	20	–	–	–	–	–	30	30	30	70	80	70	–	30	70	–	12	5
–	5	–	–	–	–	–	–	–	10	20	5	–	–	–	–	–	–	–	–	–	–	–	–	1	3	–	1	3
–	–	10	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	1	–	1	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–
1	50	60	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	1	1	–	1	1	1	–	1	–	1	1	1	1	1	1	1	–	1	1	–	1	1	1	1	1	10	3	1
–	–	–	–	–	1	1	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	1	–	–	1	3	–	–	1	3	1	–	–	–	–	–	1	–	–	–	–	–	–	–	1	1	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1	10	5	10	5	1	1	5	1	3	3	5	3	1	3	–	–	–	1	1	1	1	1	1	8	5	1	20	5
–	–	1	–	–	1	1	1	3	1	1	1	–	1	3	–	–	–	–	–	–	–	–	1	1	1	–	1	–
–	3	3	–	–	1	1	3	1	5	1	1	1	1	1	–	–	1	1	1	1	1	1	–	–	–	–	1	1
–	–	–	–	–	–	3	–	1	1	1	10	3	–	3	–	–	–	–	–	–	–	–	1	–	–	–	–	–

continued

Table 1. Vegetation types belonging to the association *Junco baltici–Schoenetum nigricantis*. Based on vegetation data from the Dutch Wadden Sea Islands, analysed with the clustering program *vg-aclus* from the program package VEGROW (Fresco 1991)—*continued*

	Ia														Ib							
	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	2	2	4	0	2	2	2	5	2	2	0	0	2	0	3	4	4	3	5	4	5	5
	1	2	6	8	4	5	6	1	7	8	6	7	0	5	7	9	4	2	3	1	5	6
Phragmitetea																						
Phragmites australis	-	-	-	-	-	-	-	1	-	-	5	-	-	-	-	-	-	-	-	-	-	-
Lythrum salicaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Mentha aquatica	-	-	-	-	-	-	-	2	-	-	3	-	-	1	-	5	1	1	-	3	3	12
Galium palustris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	1	1	-
Caricetum trin.-nigrae																						
Carex trinervis	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus flammula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Oxycoccus macrocarpos	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agrostis canina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eleocharis pal., ssp. *pal.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex nigra	-	-	-	-	-	-	-	1	-	-	-	-	-	-	5	12	-	1	5	-	8	1
Eriophorum angustifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	12	-	-	-	-
Empetro–Erecetum																						
Empetrum nigrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erica tetralix	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla erecta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudoscleropodium purum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Violo–Corynephoretum																						
Carex arenaria	-	-	-	3	-	-	-	-	-	5	3	1	-	1	-	-	-	-	-	-	-	-
Molinietalia																						
Carex panicea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus conglomeratus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lotus corniculatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holcus lanatus	-	-	1	1	-	-	-	-	-	3	1	1	-	3	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lulula campestris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Danthonia decumbens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galium uliginosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prunella vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium palustre	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Salicion cinereae																						
Salix repens	8	1	20	10	12	8	3	20	2	60	20	3	20	1	-	8	2	1	20	40	40	12
Hippophaë rhamnoides	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-
Betula pubescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

ADDENDA: *Agrostis capillaris* 253:1; *Aneura pinguis* 233:1, 248:1; *Atriplex prostrata* 207:1; *Berula erecta* 219:1; *Brachythecium rutabulum* 111:1; *Bryum* sp. 150:3; *Calammophila baltica* 246:1, 248:1; *Carex cuprina* 219:1; *Carex disticha* 185:1; *Carex riparia* 244:30; *Cirsium arvense* 146:1, 147:1, 145:1; *Centaurium littorale* 173:1; *Clenidium molluscum* 146:5; *Cynosurus cristalus* 210:3; *Equisetum palustre* 187:1, 178:1; *Eupatorium cannabinum* 206:1; *Euphrasia stricta* 145:1, 248:1; *Gentiana amarella* 244:1; *Holcus mollis* 228:1; *Hypericum quadrangulum* 145:1; *Hypnum cupressiforme* 110:5, 111:3; *Hypnum jutlandicum* 145:1; *Lathyrus pratensis* 233:1; *Lophocolea bidentata* 233:1; *Lotus uliginosus* 178:1; *Lychnis flos-cuculi* 210:3; *Lycopus europaeus* 151:1, 145:5, 117:1; *Mnium* sp. 185:10, 187:10; *Odontiles verna* 246:1, 205:1; *Oenanthe lachenalii* 145:1; *Pellia endivifolia* 251:1; *Plantago major* 181:1; *Poa pratensis* 208:1, 228:1, 171:1, 111:1, 112:1, 210:1, 233:1, 219:1; *Ranunculus repens* 173:1; *Rhytidiadelphus squarrosus* 238:1, 248:5; *Rubus caesius* 146:5, 150:1, 147:1, 145:3, 110:2; *Rubus* sp. 233:1; *Sagina nodosa* 233:1; *Sonchus arvensis* 251:1, 145:1; *Stellaria* sp. 228:1; *Taraxacum officinale* 251:1, 220:1, 210:1, 229:1; *Taraxacum palustre* 146:1, 150:1, 151:1, 147:1; *Trifolium fragiferum* 186:1; *Trifolium pratense* 186:1; *Vicia cracca* 210:1, 238:1, 219:1.

Ic					Id										Ie								If					
146	150	151	147	145	181	172	176	177	185	186	187	178	173	171	110	111	112	113	114	115	116	117	210	233	238	219	248	229
–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	3
–	–	–	–	–	3	5	1	1	3	10	1	1	3	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	1	3	1	–	1	–	1	1	1	1	1	1	1	–	–	–	–	–	–	–	–	–	1	1	3	5	12	1
–	–	–	–	–	1	1	1	1	1	1	–	–	1	1	–	–	–	–	–	–	–	–	1	1	1	1	–	1
3	1	1	1	1	1	1	1	1	–	1	5	1	1	1	1	–	1	3	10	10	10	10	–	–	–	–	–	–
–	–	–	–	–	1	1	5	3	1	1	10	10	1	1	–	–	–	–	–	–	–	–	1	–	–	1	–	–
–	–	–	–	–	1	1	–	–	–	1	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	–	–	1	1	–	1	12	7	–	–	–	–	1	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
–	1	1	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	10	3	30	10	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
–	–	–	–	–	1	1	1	1	1	1	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	3	1	3	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	3	–	–	–	12
1	–	5	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	60
–	–	–	–	–	1	–	–	–	1	–	–	–	–	1	1	1	1	1	1	1	–	–	–	1	–	–	1	1
–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	5	–	1	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
–	–	1	–	–	–	–	–	–	–	–	5	–	–	–	30	5	10	1	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	1	–	–	–	–	–	1	–	1	1	1	1	3	1	–	–	–	1	30	8	1	8	20
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	1
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	1	–	–	–	1
1	10	10	10	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	1	1	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	3	10	5	3	–	–	–	–	–	–	–	–	–	–	1	1	1	1	1	1	–	–	–	3	–	–	3	1
1	1	1	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	2	3	2	–	8	8
3	5	5	–	1	1	5	1	5	3	5	5	7	3	20	30	30	30	30	20	20	20	20	20	40	8	20	30	30
–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	10	–	2	30	30	5	2	3	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	3	1	–	1	1	–	–	–	–	–	1	1

Groundwater composition

Sets of three groundwater tubes (PVC, diameter: 18 mm) were placed at sites where soil samples were taken. The three tubes had filters of 10 cm at the following depths: 20–30, 50–60 and 90–170 cm below soil surface. Between 1987 and 1991, in the summer period (June–August), groundwater samples were taken at all sites and levels. The tubes were emptied 1 day before sampling and allowed to refill with fresh groundwater. The samples were stored in polyethylene bottles, filled to the brim, for 8 days at 4°C in a dark room. Fifty ml was adjusted to pH 2, by addition of 2·5 ml 4% HCl. Cation contents (Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}) were measured in this subsample, using a flame atomic adsorption spectrometer (AAS). One hundred ml was used for the other measurements. CO_2 and HCO_3 were measured by titration methods, Cl^-, SO_4^{2-} NO_3^-, NH_4^+ and $H_2PO_4^{2-}$ with an auto-analyser (Skalar). To check the reliability of the analyses the ion balance was calculated in relation to the electrical conductivity (EC_{25}). Unreliable analyses (a deviation in the ion balance of more than 10% or a difference in computed vs. measured EC_{25} of more than 15%) were discarded.

Data analysis

Vegetation data were analysed using the program package VEGROW (Fresco 1991). Species cover data were converted to percentages and, in order to downweigh dominant species, square-root transformed. Percentage dissimilarity was calculated between all vegetation samples (cf. Jongman *et al.* 1987). On the dissimilarity matrix an average-linkage agglomerative clustering was applied. In the resulting tables species were arranged in ecological groups according to Schaminée *et al.* (1995). Clusters dominated by species from salt marsh communities (*Armerion maritimae*) and dry communities (*Violion caninae* and *Thero–Airion*), comprising 28 plots, were ommitted from the tables.

Relationships between habitat factors and dune slack vegetation were derived from 51 sites, all sampled in June 1991. Lowest groundwater levels (LWL) were extracted from 2-weekly records of 1991, a relatively dry year: the precipitation surplus was 60 ml (measured on the island of Texel), being on average *c.* 250 ml. Other abiotic factors involved were: pH(H_2O), NaCl, total nitrogen (N-tot), total phosphorus (P-tot) and total carbon (C-el), all measured in the (organic) top layer. These data were related to vegetation composition with a canonical correspondence analysis (CCA) (Ter Braak 1986). No data transformation but downweighing of rare species was applied.

A PCA was carried out on the main ionic components which determine chemical groundwater composition (Stuyfzand 1993). The data of all sampling depths were included. Data ranges were standardized for all separate ions. The principal components obtained were Varimax rotated.

RESULTS

Vegetation

The clustering of the vegetation plots resulted in nine clusters.

Six clusters representing the younger stages are presented in Table 1. Cluster Ia contains many characteristic species of the basiphilous pioneer community *Junco baltici–Schoenetum nigricantis*, as well as many salt marsh species (*Armerion maritimae*). Cluster Ib is a species-poor variant of this *Schoenetum* community with only a low frequency and abundance of *Schoenus nigricans*. Some salt marsh species are present, but this cluster is characterized mainly by the occurrence of many species of wet and relatively eutrophic marshes (*Caricetum trinervi-nigrae* and *Phragmitetea*). Cluster Ic is a *Schoenetum* type with a well-developed moss layer. *Juncus subnodulosus* and *Schoenus nigricans* are abundant in this vegetation type. Species from open and drier habitats (*Danthonia decumbens*, *Prunella vulgaris*, *Potentilla erecta* and *Rubus caesius*) have a high frequency here. Cluster Id has several species of the pioneer community *Samolo–Littorelletum*, such as *Samolus valerandi* and *Littorella uniflora*, but also has species of acid dune heath (*Empetrum nigrum*) and species from the small sedge community *Caricetum trinervi-nigrae*. Except for *Schoenus nigricans* itself, only a few *Schoenetum* species are present, and with low frequencies. Cluster Ie is a moist *Schoenetum* without *Schoenus nigricans* but with an abundance of *Epipactis palustris* and *Equisetum variegatum*. No acidophilous species are present but woody plant species, such as *Salix repens*, *Hippophaë rhamnoides* and *Betula pubescens* are frequent. Cluster If represents an older stage of *Schoenetum* with high frequencies of *Caricion nigrae* and *Molinietalia* species, showing the influence of a long-lasting mowing regime. *Schoenetum* species are scarce, but *Pedicularis palustris* is frequent.

The remaining clusters (Table 2) represent later successional stages. Cluster II represents clearly a *Calamagrostis epigejos–Ophioglossum vulgatum* frame community with abundant *Oxycoccus macrocarpos* and some *Empetro–Ericetum* species. This cluster is characteristic of older dune slack vegetation, especially on the islands of Terschelling and Vlieland (Westhoff & Van Oosten 1991). Cluster III characterizes an older successional stage with many *Phragmitetea* species, indicating wet conditions. Cluster IV represents an older stage with a high abundance of *Carex nigra*.

Vegetation and soil factors

The results of a CCA on vegetation data, lowest groundwater levels and soil factors are shown in a biplot of the first two axes extracted (Fig. 2). The scale for vegetation plots (u-scale) differs from the one for abiotic factors (c-scale). The arrows represent the abiotic factors used in the analysis. The direction and length of the arrows correspond with the direction and magnitude of greatest variation in the total dataset. When plot points are projected perpendicularly to the (prolonged) arrows, their order represents approximately the ranking of weighted averages with respect to the values of the factors involved. A projection at the same side of the origin as the head of the arrow implies a value higher than average, a projection at the opposite side implies a value lower than average. Vegetation plots are given as representatives of the distinguished vegetation clusters.

The eigenvalues of the first two axes are 0·62 resp. 0·59, making the biplot account for 54% of the total variance of weighted averages (the sum of canonical eigenvalues of all extracted axes). The species–environment correlations for the first two axes are high (0·89 resp. 0·92). These results suggest a strong association between vegetation and environmental variables in the biplot presented (cf. Jongman *et al.* 1987).

The first axis can be interpreted as a moisture gradient, the second axis as a pH gradient; the correlation of the LWL with the first axis is −0·78 and of the pH with the second axis 0·86. The variation in $CaCO_3$ content is related closely to the pH variation in the topsoil; it does not, however, account for much variation in the dataset. Total nitrogen and phosphorus concentrations and the percentage carbon, being highly correlated (corr. coeff. N-P: 0·94, N-C: 0·96 and P-C: 0·92), account for less variation

Table 2. Vegetation types succeeding *Junco baltici–Schoenetum nigricantis* vegetation. Based on vegetation data from the Dutch Wadden Sea Islands, analysed with the clustering program VG-ACLUS from the program package VEGROW (Fresco 1991)

	II									III								IV												
	191	179	180	182	183	184	174	175	190	127	128	129	130	131	124	125	126	235	230	231	211	239	216	252	155	154	234	218	236	240
Armerion maritimae																														
Scirpus maritimus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	20	–	–	–	–	–	–
Juncus gerardii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	1	–	1
Festuca rubra	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nanocyperion flavesc.																														
Carex oederi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Sagina procumbens	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Junco baltici–Schoenetum nigricantis																														
Schoenus nigricans	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Eleocharis quinqueflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Dactylorhiza incarnata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Carex flacca	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Juncus subnodulosus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Juncus alpinoarticulatus	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	1	–	3	12	1	1	–	–	–	–	1	–
Pedicularis palustris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–	–
Calliergonella cuspidata	–	–	–	–	–	–	–	–	–	–	–	–	5	10	–	–	–	–	12	1	–	12	–	–	–	–	30	–	–	–
Campylium sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	1	–	3	–	–	1	–	–	1
Drepanocladus aduncus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	1	–	5	1	–	–	–
Frame community of:																														
Calamagrostis epigejos	10	70	20	20	1	3	20	3	40	–	–	–	3	–	–	–	–	–	–	–	–	5	–	–	3	1	1	–	–	–
Ophioglossum vulgatum	–	1	–	3	–	–	3	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lolio–Potentillion																														
Agrostis stolonifera	–	–	–	–	1	–	–	–	–	1	1	1	1	1	5	3	1	–	1	–	3	–	–	1	–	–	3	–	–	5
Eleocharis pal., ssp. *unigl.*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	5	5	–	3	–	1	–	–	–	–	–	–
Hydrocotyle vulgaris	–	–	1	1	1	–	–	–	1	1	3	–	1	1	10	5	–	–	1	1	1	1	–	5	–	–	1	1	1	1
Potentilla anserina	3	3	1	1	1	–	1	1	1	–	–	–	10	10	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–

continued

Table 2. Vegetation types succeeding *Junco baltici–Schoenetum nigricantis* vegetation. Based on vegetation data from the Dutch Wadden Sea Islands, analysed with the clustering program VG-ACLUS from the program package VEGROW (Fresco 1991)—*continued*

	II									III								IV												
	191	179	180	182	183	184	174	175	190	127	128	129	130	131	124	125	126	235	230	231	211	239	216	252	155	154	234	218	236	240
Calthion palustris																														
Carex disticha	–	–	–	–	–	–	–	–	–	40	60	60	60	50	70	80	50	–	–	–	–	–	–	–	–	–	–	–	–	–
Caltha palustris	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phragmitetea																														
Phragmites australis	–	–	–	–	–	1	–	–	–	30	–	–	–	–	1	1	20	–	–	–	1	3	1	5	–	–	–	5	–	8
Lythrum salicaria	1	–	–	1	1	3	1	1	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	1	–
Iris pseudacorus	–	–	–	–	–	–	–	–	–	–	–	3	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Equisetum fluviatile	–	–	–	–	–	–	–	–	–	1	1	1	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Polygonum amphibium	–	–	–	–	–	–	–	–	–	1	1	1	1	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Mentha aquatica	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	1	1	1	1	–	1	–	–	1	–	–	–
Galium palustre	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	1	–	5	1	1	–	1	1	1	1	–	–
Caricetum trin.-nigrae																														
Carex trinervis	1	–	3	1	1	1	1	1	1	–	–	–	1	3	–	–	–	–	1	1	–	–	–	1	1	1	–	–	–	–
Ranunculus flammula	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	1	–	1	–	1	1	–	–	–	3	1	–
Oxycoccus macrocarpos	70	1	30	30	50	60	12	60	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleocharis pal., ssp. pal.	–	–	–	–	–	–	–	–	–	3	1	3	–	–	1	1	1	–	–	–	1	–	1	–	–	–	–	10	–	–
Carex nigra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	47	12	10	20	30	8	–	–	1	1	–	8
Menyanthes trifoliata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	1	40	–	–	–	–	–	–	–	–	–	–	–	–
Potentilla palustris	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	40	60	8	–	1	–
Eriophorum angustifolium	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	5	–	–	–
Empetro–Ericetum																														
Empetrum nigrum	–	–	–	5	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erica tetralix	–	–	–	–	10	30	–	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Potentilla erecta	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Violo–Corynephoretum																														
Carex arenaria	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

continued

Table 2. Vegetation types succeeding *Junco baltici–Schoenetum nigricantis* vegetation. Based on vegetation data from the Dutch Wadden Sea Islands, analysed with the clustering program VG-ACLUS from the program package VEGROW (Fresco 1991)—*continued*

	II									III								IV												
	191	179	180	182	183	184	174	175	190	127	128	129	130	131	124	125	126	235	230	231	211	239	216	252	155	154	234	218	236	240
Molinietalia																														
Carex panicea	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–
Juncus conglomeratus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–
Holcus lanatus	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cirsium palustre	–	–	–	–	–	–	1	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Salicion cinereae																														
Salix repens	5	7	30	20	20	5	40	12	30	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	10	10	8	–	1	–
Hippophaë rhamnoides	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sphagnum squarrosum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	70	1	–	–	–	–

ADDENDA: *Agrostis capillaris* 216:1; *Berula erecta* 211:1; *Calystegia sepium* 131:1; *Cardamine pratensis* 130:1, 131:1, 230:1, 252:1; *Carex cuprina* 235:1, 234:5, 240:3; *Chara* sp. 218:1; *Cirsium arvense* 129:1; *Drepanocladus* sp. 130:1; *Epilobium palustre* 211:1, 240:1; *Equisetum palustre* 191:1; *Hippuris vulgaris* 235:1, 218:1, 236:5; *Juncus arcticus* 183:1; *Juncus articulatus* 231:1; *Lemna minor* 128:1, 129:1; *Lotus uliginosus* 175:1, 131:1; *Lychnis flos-cuculi* 183:1; *Lycopus europaeus* 131:1; *Mnium* sp. 130:5; *Myosotis palustris* 131:1, 126:1, 211:1; *Plagiomnium ellipticum* 131:1; *Poa pratensis* 191:1, 179:1, 182:1, 174:1, 190:1, 211:1; *Ranunculus lingua* 128:1, 130:1; *Ranunculus repens* 130:1; *Rhinanthus angustifolius* 131:1; *Rumex crispus* 218:1; *Rumex hydrolapathum* 128:1, 129:1; *Scirpus cariciformis* 235:1; *Scirpus rufus* 231:8; *Scutellaria galericulata* 130:10, 131:1; *Senecio jacobea* 131:1; *Sonchus arvensis* 128:1, 130:1, 131:1; *Taraxacum officinale* 131:1; *Viona canina* 182:1.

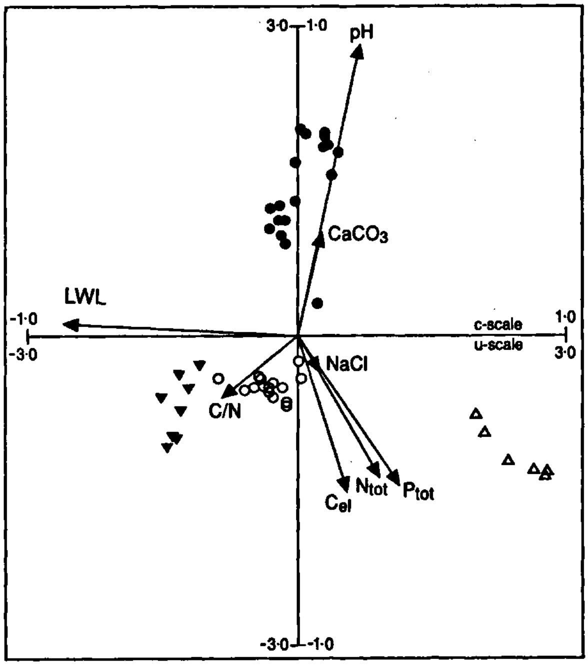

Fig. 2. Canonical correspondence analysis (explanation in the text). All vegetation samples involved are attributed to the plant communities dominating the vegetation clusters from Tables 1 and 2: ●, *Junco baltici–Schoenetum nigricantis* (clusters I): ▼, *Ophioglosso–Calamagrostietum epigeji* (cluster II): △, *Phragmitetea* (cluster III); and ○, *Caricetum nigrae* (cluster IV). LWL = lowest water level.

on the first two axes than do groundwater levels and pH values. However, these factors explain most of the variation on the third axis of the CCA, having an eigenvalue of 0·32 (thus explaining an additional 14% of the total variance of weighted averages). Variations in NaCl content play a minor role within the dataset.

Schoenetum stands are clearly related to high pH values. Cluster III, with many *Phragmitetea* species, is strongly associated with high values of C, N and P. Their positions at the opposite end of the LWL arrow indicate that nutrient-rich dune slack habitats mainly occur under wet circumstances. Another older succession stage dominated by *Calamagrostis epigejos* (cluster II) is found at the opposite end of the pH arrow, closely associated with heathland species such as *Erica tetralix*, *Calluna vulgaris* and *Oxycoccus macrocarpos*. Its position relates to average nutrient contents, but it is clearly correlated with a high C/N ratio. *Caricetum nigrae* stands (cluster IV) are in an intermediate position between the other two older succession stages.

Groundwater composition

The results of the PCA analysis on the total dataset (102 water samples) are presented in Table 3. The first axis explains 77% of the variance. The second axis explains 11% of the variance (Table 3a). All chemical constituents considered have comparable high loadings on the first axis (Table 3b). These results show one common factor which outweighs other possible influences, making concentrations of all cat- and anions simultaneously rise and fall. This factor appears to be the amount of brackish water

Table 3. Results from a PCA analysis with the computer program SPSS on the chemical composition of 102 shallow groundwater samples from seven dune slacks on the Dutch Wadden Sea Islands: (a) gives the percentages of variance accounted for by each factor; (b) shows the loadings of each variable on the first axis

(a) Factor	Explained % of variance	Cumulative explained % of variance
1	77·4	77·4
2	10·8	88·2
3	6·1	94·2
4	3·4	97·7
5	1·9	99·6
6	0·4	100·0

(b) Variable	Loading on first component
Cl^-	0·95
HCO_3^-	0·82
SO_4^{2-}	0·66
Ca^{2+}	0·87
Mg^{2+}	0·92
Na^+	0·96
K^+	0·93

merging with fresh water, thus dominating the chemical composition of the water samples.

The PCA analysis has been repeated on a freshwater data set of 76 water samples which remained after the exclusion of all samples with Cl^- concentrations above 200 mg/l. Three axes have been extracted, explaining 55, 17 and 15% of the variance (Table 4a). After rotation these axes present a clear picture of the factors distinguishing fresh groundwater types (Table 4b). Ca^{2+} and HCO_3^- concentrations have high loadings on the first axis. Na^+ and Cl^- concentrations correlate best with the second axis. SO_4^{2-} and K^+ concentrations have the highest loadings on the third axis.

Cross-sections

Three dune slack cross-sections are depicted in Figs 3–5, illustrating the spatial relations between vegetation, soil factors and groundwater composition in respectively a brackish primary dune slack after 100 years of succession, a secondary dune slack after 40 years of succession and an acidified, *c.* 400 years old, primary dune slack. The presence of some rare and protected species and of the plant communities, distinguished in the cluster analysis (cf. Tables 1 and 2), are clearly related to the pH of the topsoil layer and to the percentage of $CaCO_3$ in the mineral subsoil and/or the concentrations of Ca^{2+} and Cl^- in shallow groundwater.

DISCUSSION

Vegetation and habitat conditions

The six vegetation clusters with basiphilous pioneer species (Table 1) represent plant communities (or contain elements of them) which are also distinguished in previous,

Table 4. Results from a PCA analysis as in Table 3 for 76 samples with fresh ($Cl<5$ meq./l.) shallow groundwater: (a) as Table 3(a); (b) shows the loadings of each variable on the first three axes

(a) Factor	Explained % of variance	Cumulative explained % of variance
1	54·6	54·6
2	17·3	71·9
3	14·6	86·5
4	8·9	95·4
5	3·7	99·1
6	0·7	99·7
7	0·3	100·0

(b) Variable	Loading on first component	Loading on second component	Loading on third component
Cl^-	0·17	0·95	0·20
HCO_3^-	0·96	0·15	0·14
SO_4^{2-}	0·09	0·13	0·85
Ca^{2+}	0·93	0·21	0·14
Mg^{2+}	0·51	0·36	0·68
Na^+	0·22	0·93	0·23
K^+	0·09	0·17	0·76

more extensive vegetation descriptions of wet dune slack vegetation on the Dutch Wadden Sea Islands (Westhoff 1947; Van Zadelhoff 1981; Westhoff & Van Oosten 1991). All clusters contain elements of the association *Junco baltici–Schoenetum nigricantis*. They reflect both edaphic variation and successional changes within this association. Clusters Ia and Ib, for instance, harbouring many salt marsh species (*Armerion maritimae*) indicate brackish conditions while Ic and Id with many pioneer species of the communities *Nanocyperion* and *Samolo–Littorelletum* reflect freshwater influences. In the clusters Ib, Id, Ie and If there is a high frequency of species of succeeding developmental stages ranging from reeds (*Phragmitetea*) to grassland communities (*Molinietalia*). Basiphilous species occur in low frequencies in the clusters II, III and IV (Table 2) which represent the older successional stages of the dune slack hygroseres (the *Calamagrostis epigejos–Ophioglossum vulgatum* frame community, *Phragmitetea*, respectively *Caricetum nigrae*).

CCA shows that older successional stages are related to more acid conditions and higher nutrient contents than *Schoenetum* stands, which is in line with earlier findings (De Vries 1961; Willis 1963; Koerselman 1992). The community dominated by *Calamagrostis epigejos* indicates drier conditions than the *Schoenetum* community. This corresponds with the experimental observations of Van Beckhoven (1995) that *Calamagrostis epigejos* is competitive towards *Schoenus nigricans* under moist rather than wet conditions. The older stages in the Koegelwieck chronosequence show that vigorous growth of *Calamagrostis epigejos* leads to a surface rise of *c.* 10 cm (unpublished data) and thus to drier conditions. This surface rise is caused by accumulating organic matter which, due to acidification, has a high C/N ratio. This probably explains the association of the *Calamagrostis epigejos–Ophioglossum vulgatum* frame community with relatively

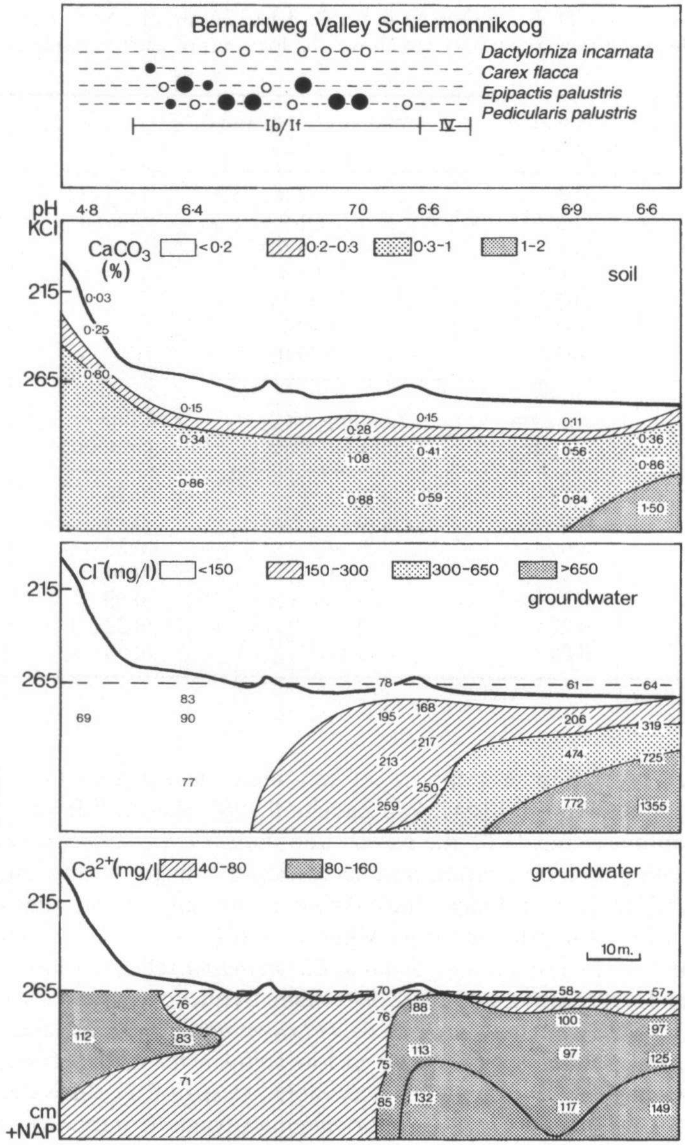

Fig. 3. Bernhardweg valley, Schiermonnikoog. Ib, If and IV correspond to the vegetation clusters of Tables 1 and 2. Freqencies of occurring species: ● = abundant, • = frequent, o = occasionally.

low groundwater levels and high C/N quotients (Fig. 2). *Phragmitetea* stands clearly indicate wetter conditions and a higher nutrient availability than *Schoenetum* stands. *Caricetum nigrae* stands have an intermediate position and represent a successional change from *Schoenetum* to *Phragmitetea* communities under wet conditions (cf. Westhoff & Van Oosten 1991).

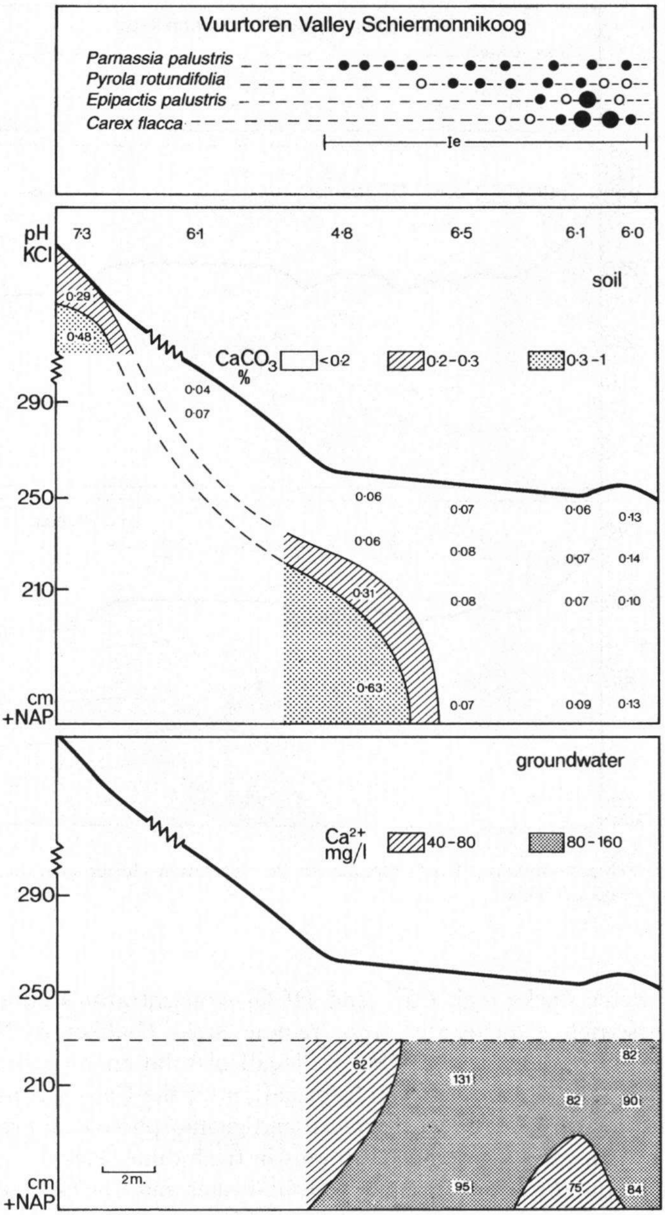

Fig. 4. Vuurtoren valley, Schiermonnikoog. Ie corresponds to the vegetation cluster of Table 1. Frequencies of occurring species: ● = abundant, • = frequent, ○ = occasionally.

Key environmental variables

The groundwater composition of dune slacks on the Dutch Wadden Sea Islands shows a major influence of brackish surface water or salt spray (cf. Stuyfzand 1993). Even in the 'freshwater' dune slacks, where Ca^{2+} and HCO_3^- are the dominant ions, Na^+ and Cl^- concentrations determine the second axis. Here the influence of salt spray is evident.

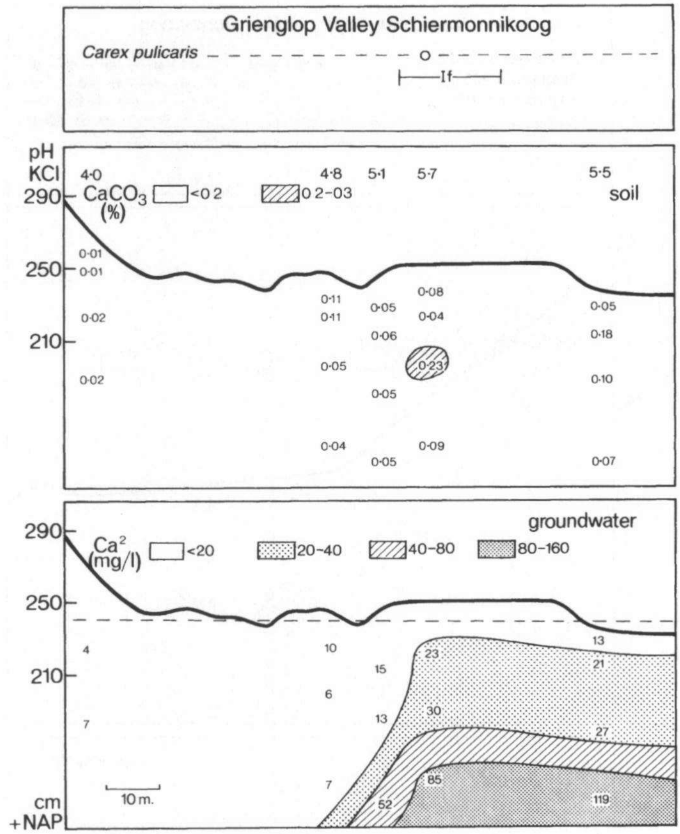

Fig. 5. Griënglop, Schiermonnikoog. If corresponds to the vegetation cluster of Table 1. Frequency of occurring species: o = occasionally.

In the freshwater slacks high Ca^{2+} and HCO_3^- concentrations either indicate exfiltration of base-rich groundwater from remote areas (Bakker & Nienhuis 1990; Stuyfzand 1993; Grootjans *et al.* 1996) or (local) dissolution of carbonate minerals (Rozema *et al.* 1985; Sival *et al.* 1997). Information on the $CaCO_3$ content in the soil is needed to distinguish between hydrological and geomorphological processes causing high shallow groundwater Ca^{2+} concentrations in fresh dune slacks.

Cl^{-} and Ca^{2+} concentrations in shallow groundwater and $CaCO_3$ content of the soil can thus be considered as key environmental variables for the assessment of restoration perspectives for basiphilous pioneer communities in dune slacks. They represent environmental processes controlling important mechanisms in the rooting zone.

Within the range of dune slack habitats the mean groundwater level and its seasonal variation is also supposed to indicate the perspectives for different plant communities (Van der Laan 1979; Bakker 1990; Grootjans *et al.* 1988, 1991; Lammerts *et al.* 1995). However, within the investigated dataset, the groundwater level does not represent a key environmental variable. It differentiates better between the older dune slack communities as it does between between basiphilous dune slack vegetation, on one hand, and other dune slack communities on the other hand (Fig. 2). Probably a more detailed analysis of groundwater regimes may reveal hydrological parameters indicating (periodic) seepage areas responsible for buffering by exfiltrating groundwater (Grootjans *et al.* 1996; Sival *et al.* 1997).

The three cross-sections (Figs 3–5) illustrate that the three key variables proposed, if used complementarily, explain the presence/absence of basiphilous pioneer vegetation adequately. It is expected that these variables are also helpful in selecting dune slacks with prospects for the regeneration of basiphilous pioneer vegetation. It must be realized, however, that successful establishment of basiphilous pioneer vegetation also depends on the amount of organic matter, soil pH, light penetration and the presence of a seed bank. As a consequence the specification of restoration measures, e.g. hydrological restoration, sod cutting and management measures (mowing, grazing and introduction of species), must be based on additional information on these factors.

The life span of basiphilous pioneer vegetation

The effects of restoration measures also depend on the expected life span of basiphilous pioneer communities.

For primary dune slacks, in which the initial lime content is comparable, a life span of basiphilous pioneer vegetation with some general validity probably can be derived. Eisma (1968) gave arguments for sytematic differences in initial lime content along the Dutch coastline between the coastal areas north and south of Bergen, but not for differences within the northern Wadden Sea area. For the North Sea beaches in the Dutch Wadden Sea area the initial lime content is between 0·5 and 1·0% (Westhoff & Van Oosten 1991).

The Strandvlakte, Bernhardweg valley, Moksloot valley and Griënglop may be considered to represent different stages of a chronosequence after 30, 100, 200 and 400 years, respectively, of vegetation development (Fig. 6). In this chronosequence the soil pH remains around neutral and basiphilous pioneer vegetation persists for over 100 years under a mowing regime. Some individual basiphilous species can even persist for over 200 years when the top layer is completely decalcified, probably because inundation with brackish water or discharge of calcareous groundwater maintains the soil pH around 6. Without a mowing regime basiphilous pioneer communities reach their optimum after *c.* 25 years, decline after 35 and disappear within 100 years.

Differences between hydrological regimes and geomorphological history are expected to be larger in secondary slacks than in primary slacks. The life span of basiphilous pioneer communities is, therefore, also expected to show larger differences. A comparison of the secondary slacks Koegelwieck and Loodsmansduin valley illustrates this. In the Koegelwieck, in a sod-cutting experiment executed in 1956, an 8 cm thick top layer with *c.* 20% organic matter developed after 35 years of succession. The soil pH decreased from 7·0 to 4·5 and basiphilous pioneer vegetation almost completely disappeared. In the Loodsmansduin valley a 12–15 cm thick top layer with less than 10% organic matter has developed after *c.* 200 years of succession. The soil pH still is above 7·0 due to the presence of exceptionally high concentrations of $CaCO_3$ (*c.* 20%) locally in the topsoil layer. In this slack basiphilous pioneer vegetation was out competed by high productivity grasses and shrubs such as *Rubus caesius*, but it regenerated soon after a mowing regime had started in 1982. The organic matter accumulation rate and composition apparently plays a crucial role (cf. Olff *et al.* 1993; Lammerts *et al.* 1995). Features of organic matter (accumulation) may in turn depend on differences in hydrological and

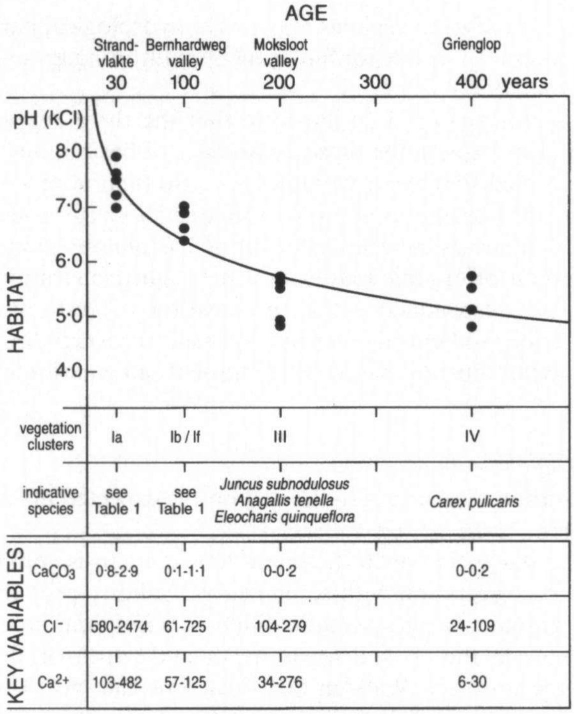

Fig. 6. Changes in key parameters during succession in primary dune slacks. A log-fitted curve has been fitted through the pH data. The vegetation clusters correspond with Tables 1 and 2. For the ranges given for the key parameters only data are used from the upper soil layers (up to 1 m below surface). $CaCO_3$ % is measured in the mineral subsoil, Ca^{2+} and Cl^- concentrations (mg/l) in the shallow groundwater.

geomorphological processes. Grootjans *et al.* (1995) suggested that the Loodsmansduin valley and the Koegelwieck have different hydrological regimes. The Loodsmansduin valley is, or probably was, located in a very strong exfiltration zone of a large hydrological system (even leading to secondary calcite deposits; Sival 1997), while the Koegelwiek is fed by water from a local hydrological system, exfiltrating only during extremely wet periods.

It may be concluded that for secondary dune slacks the differences in life span of a basiphilous pioneer community can be considerable, due to differences in hydrological regimes and also, perhaps, in initial lime content of the soil.

Perspectives for nature management

Although a substantial decline in basiphilous pioneer vegetation has occurred in the last 20–40 years, there are some good opportunities for regeneration of suitable habitats, especially in young slacks influenced by periodic inundation by brackish water. When in the younger parts of the islands time and space are guaranteed for dynamic dune-forming processes these slack types will show a balance between rise and decline of various plant communities which offers perspectives for many basiphilous pioneer species, also on a long-term basis.

In older dune areas of the Wadden Sea Islands basiphilous pioneer vegetation can be maintained only on very specific sites where exfiltration of calcareous groundwater is the dominating process. Infiltration areas, feeding these slacks, should be conserved or restored carefully by maximizing infiltration, e.g. by removing any drainage or by thinning or removing forest plantations (thus minimizing evaporation). Some additional management, mowing or periodical sod cutting, may be necessary in the slacks itself.

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