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Mesotrophic basiphilous communities affected by changes in soil properties in two dune slack chronosequences

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SUMMARY

Two soil chronosequences were investigated to identify soil properties related to acidification during succession of dune slack vegetation. One chronosequence was associated with a primary succession series on a wet beach plain on the Dutch island of Schiermonnikoog, the other with a succession series after sod cutting in a secondary (blown out) slack on the island of Terschelling (the Koegelwieck).

Both chronosequences include a succession sequence which starts from bare sand, proceeds to basiphilous, mesotrophic (low productivity) vegetation types (Junco baltici–Schoenetum nigricantis) with many rare species, and ends with productive shrubbery or forested, acidified organically enriched soils with little floristic value. The pH decreased with time in both chronosequences. In the beach plain this was correlated with an increase in organic matter and a decrease in salt content. In the blown out slack the pH decrease was correlated with an increase of organic matter and with an increase in exchangeable bases, except for Ca, on the exchange complex. The faster organic matter increase and pH decrease in the blown out slack chronosequence resulted in a relatively short persistence of mesotrophic vegetation type with endangered basiphilous species. The mesotrophic basiphilous vegetation persists for a longer time (*c.* 20–25 years) in the initially calcareous beach plain chronosequence with a high acid buffering capacity as compared to the Koegelwieck chronosequence with a low acid buffering capacity.

Key-words: buffer capacity soil, $CaCO_3$, organic matter, pH, *Schoenus migricans*, sod removal.

INTRODUCTION

Young dune slacks, depressions in dune systems which are flooded during the winter and most of the spring, harbour many rare and endangered plant species and contribute significantly to the floristic value of the NW European coastal area in general and the Wadden Sea domain in particular (Grootjans *et al.* 1988; Lammerts *et al.* 1992, 1995;

Nomenclature follows Van der Meijden *et al.* (1990) for plants and Westhoff & Den Held (1969) for plant communities.

Westhoff *et al.* 1993). These species are particularly present in low-productive, basiphilous dune slack communities of the early stages of vegetation succession (Samolo–Littorelletum, Parnassio–Juncetum atricapilli and Junco baltici–Schoenetum nigricantis).

During the last few decades these plant communities have disappeared in the coastal area due to both anthropogenic and natural causes (Van Dijk & Grootjans 1993). The basiphilous dune slack communities have rapidly turned into *Salix*-dominated shrublands (Van Dorp *et al.* 1985) or into communities characteristic of acidified soil conditions in most dune areas (Grootjans *et al.* 1991). During soil development increasing amounts of organic matter and nutrients as nitrogen and phosphorus and decreasing pH create opportunities for rapid growing species which replace the plant species of the early stages of vegetation succession. The persistence of mesotrophic basiphilous plant species was therefore thought to depend on soil properties, such as the acid buffering capacity and the organic matter dynamics of the system (Olson 1958; Olff *et al.* 1993).

In order to understand the soil characteristics important to maintain basiphilous species in wet dune systems it therefore seems necessary to concentrate on the buffer ranges for the plant communities concerned in relation to the rate of accumulation of organic matter. The objective of the present study is to describe the development of soil properties such as the buffer capacity and organic matter content of sandy dune slack soils during ecosystem development. For this purpose two successional soil sequences were compared, both including vegetation stages with mesotrophic basiphilous species, but differing in initial lime content and in hydrology. Because mesotrophic basiphilous dune slack plants are confined to sandy nutrient-poor habitats with non-acidified rooting zones (pH higher than 5; Lammerts *et al.* 1995), the relevant buffers are the $CaCO_3$ and the cation exchange complex (Ulrich 1981; Bruggenwert *et al.* 1991). The silicate buffer is ignored due to the low silicate dissolution rate (Eisma 1968; De Vries *et al.* 1994).

MATERIAL AND METHODS

Site description

Two successional soil/vegetation sequences were selected in 1991 on the Frisian Islands of Schiermonnikoog (53°29'N, 6°12'E) and Terschelling (53°24'N, 5°20'E) (Fig. 1). The sequence on Schiermonnikoog included four sites of different stages of development which are interpreted from aerial photographs in combination with vegetation data of a permanent transect: 19, 32, 100 and 200 years (Olff *et al.* 1993). The first establishment of plant species is taken as the 'time-zero' for the chronosequence. The youngest two sites were located in a primary beach plain. The colonization of plant species started after the beach plain was cut off from the sea by the construction of a sand dike in 1959. Tidal influences were thereby reduced. Heavy storms in 1972, however, created a large gap in the dike which is still open. The youngest sites are flooded by the sea during the winter and early spring. This seawater may stay in the former beach plain for months. From May to September the water table may drop to 1·0 m below the soil surface in very dry summers (Olff *et al.* 1993). The oldest two sites are situated at the western side of the naturally formed sand dunes: the Kobbeduinen (100 years) and the Kooiduinen (200 years). During the winter and early spring, high ground water levels create fresh-water flooding conditions for several months.

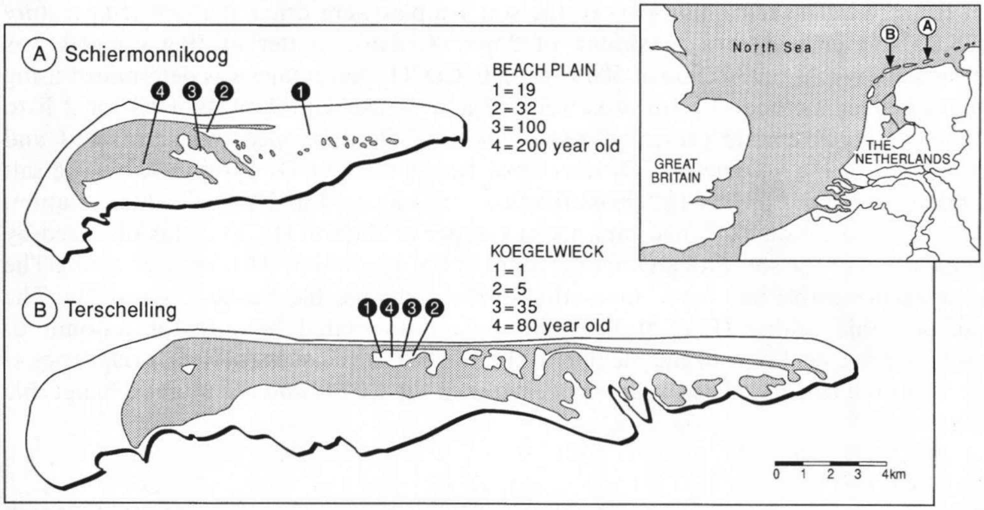

Fig. 1. (A) The location of the study sites situated on Schiermonnikoog. (B) The location of the study sites situated on Terschelling. The dark stippled area represents the dunes.

The study area on Terschelling, the Koegelwieck, is situated in the middle of the island (Fig. 1). The slack became vegetated after the restoration of a large gap in the sand dike due to heavy storms of *c.* 1910. In 1956 a decline in basiphilous species prompted the terrain managers to remove the organic enriched mineral top layer. The basiphilous species recovered well and the sod cutting was repeated in 1986 and in 1990. This led to the formation of different soil/vegetation plots, forming a development sequence spanning 80 years. In the winter the area is flooded with freshwater. In May the water table usually drops below the soil surface to reach a depth of 50 cm by the end of September.

Two plots of 2×2 m^2 were laid out near the soil sample sites of the two soil sequences to describe the abundance of the character plant species of the alliances (Westhoff & Den Held 1969) using the Londo scale of abundance (Londo 1974).

The parent materials of both chronosequences consist of mainly fine (105–150 μm) to medium (150–210 μm) well-sorted quartz sand with a mixture of 5% of other minerals including calcite (only Schiermonnikoog; 1·1%) and feldspar. The calcium carbonate consists of mainly two components: mollusc shells and detrital calcite grains (Eisma 1968). The soil profiles comprise an organic litter layer (O horizon), a dark coloured, organically enriched mineral surface horizon (A horizon) and a mineral subsoil (C horizon). The soils are classified as Arenosols (FAO/Unesco 1981) or Udipsamments (Soil Survey Staff 1975).

Sampling methods and analytical procedures

In July 1991, 30 soil samples were taken from each of the O and A horizons (total depth) and the C horizon (15–20 cm depth). Ten soil samples were pooled per horizon and mixed, resulting in three mixed soil samples per horizon and site. The depth of the present soil horizons was measured and the colour was described on moist soil samples using Munsell Colour Charts. The bulk density (mass/volume) was measured with a 100 cm^3 volume pF-ring. pH(H_2O) was determined after adding 20 ml of water to 15 g of fresh soil. The remaining part of the soil samples were dried at room temperature (25°C) and ground to a maximum of 2 mm. Organic matter in 10 g samples was measured by loss-on-ignition at 500°C for 3 h. $CaCO_3$ percentage was determined using the Scheibler method: 3 g soil was weighed and mixed with 7 ml 4M HCl for 2 h to dissolve the carbonate present. The volume of CO_2 developed, was measured and compared to the volume of CO_2 developed from pure $CaCO_3$ (Bruin 1937). The salt content, expressed as NaCl (% mass fraction) was analysed in a 1:8 soil:water solution. The effective cation exchange capacity at the pH of the soil (ECEC) was obtained by percolation of the soil with an unbuffered 0·1 M $BaCl_2$ solution (Houba *et al.* 1988). The total exchangeable bases is a summation of the exchangeable Na, K, Ca and Mg. The exchangeable acidity (EA) of the soil was not measured because the amount of exchangeable acidity is negligible due to the soil pH of the sites (pH>4·5) (De Vries *et al.* 1994) but calculated as the difference between the ECEC and the total exchangeable bases.

Data analyses

The effect of age of the individual soil horizon on the soil properties pH(H_2O), NaCl (%), $CaCO_3$ (%), organic matter (kg m^{-2}), ECEC ($mmol_c$ kg^{-1}) and exchangeable bases ($mmol_c$ kg^{-1}) were statistically tested by a one-way analysis of variance with Student–Newman–Keuls contrast among means. The dependent variable was transformed prior to the analyses if this improved the homogeneity of variances.

Interaction between the soil parameters pH(H_2O), NaCl (%), $CaCO_3$ (%), organic matter (kg m^{-2}, ECEC ($mmol_c$ kg^{-1}) and exchangeable bases ($mmol_c$ kg^{-1}) were statistically tested by linear correlation.

RESULTS

Beach plain sequence on Schiermonnikoog

Development of the vegetation. The 19-year old site is sparsely vegetated with salt-marsh species *Juncus gerardi*, *Glaux maritima* and *Salicornia europaea* (Table 1). Mesotrophic basiphilous species, such as *Schoenus nigricans*, with orchid species, e.g. *Liparis loeselii* as well as other rare species, e.g. *Parnassia palustris* cover the soil of the 32-year-old site. The two oldest sites are densely covered with trees, mainly *Betula pubescens* and *Salix repens* (100-year site) and *Betula pubescens* and *Alnus glutinosa* (200-year site).

Development of soil horizons. The development of the horizons of the four soils investigated started on a saline mineral sediment enriched with calcium carbonate. An organically enriched mineral surface horizon (A) (10 YR 2/1; black) developed on the mineral subsoil (C) (2·5 Y 5/2; greyish brown) of the four sites and on the 100- and 200-year-old sites also an organic litter layer (O) (10 YR 3/2; very dark greyish brown) (Fig. 2). The average depth of the organically enriched mineral surface horizon (A) and the organic litter layer (O) increased with age.

Chemical conditions of the soil layers. Except for the C horizon of the 19-year-old-site, all sites described are desalinized down to 20 cm depth (around 0·03% NaCl) (Fig. 2).

The amount of organic matter in the A horizon slightly increased from the 19-year-old site to the 32-year-old site (Fig. 2). In the next 45 years organic matter increased four-fold and between the 100- and 200-year-old sites organic matter further

Table 1. Character plant species and their abundance (%) in the two chronosequences

Chronosequence age (year)	Beach plain (%)				Koegelwieck (%)			
	19	32	100	200	1	5	35	80
Species of salt-marshes								
Salicornia europaea	1							
Suaeda maritima	1							
Puccinellia maritima	1							
Juncus gerardi	40							
Glaux maritima	10	1						
Species of mesotrophic calcareous dune slacks								
Schoenus nigricans		50				10		
Parnassia palustris		1						
Liparis loeselii		1						
Eleocharis quinqueflora						1		
Juncus alpinoarticulatus		1			1	1		
Centaurium littorale					1	1		
Centaurium pulchellum	1							
Samolus valerandi					1	1		
Species of oligotrophic heathland								
Erica tetralix							20	
Oxycoccus macrocarpos							60	70
Species of mesotrophic marshes								
Agrostis stolonifera	1	1	1	1				
Potentilla anserina		1	1			1	1	1
Hydrocotyle vulgaris		1		1	1			
Ranunculus flammula					1	1		
Juncus articulatus					1	1		
Carex trinervis						1	1	1
Species of eutrophic marshes								
Mentha aquatica		1			1	1		
Lythrum salicaria						1	1	1
Calamagrostis epigejos		1	1	1		1	1	10
Species of shrubs and forests								
Salix repens		1	10			1	10	1
Betula pubescens		1	40	40				
Alnus glutinosa				10				

increased to 18·5 kg m^{-2}. The amount of organic matter in the O horizon of the oldest two sites was lower than in the A horizon, but also increased with age.

During the first 100 years of soil development the pH(H_2O) remained relatively constant at around 7 in both the O and the A horizons, and at slightly higher values in the C horizon (Fig. 3). The litter layer present at the 100-year-old site had a slightly lower pH than the A and C horizon. After 200 years the pH had dropped to 4·7 in the litter layer, to 4·8 in the A and to 5·7 in the C horizon.

The percentage of $CaCO_3$ in the C horizon was relatively high in the 19- and 32-year-old sites, whereas the 100- and 200-year old sites were completely decalcified in

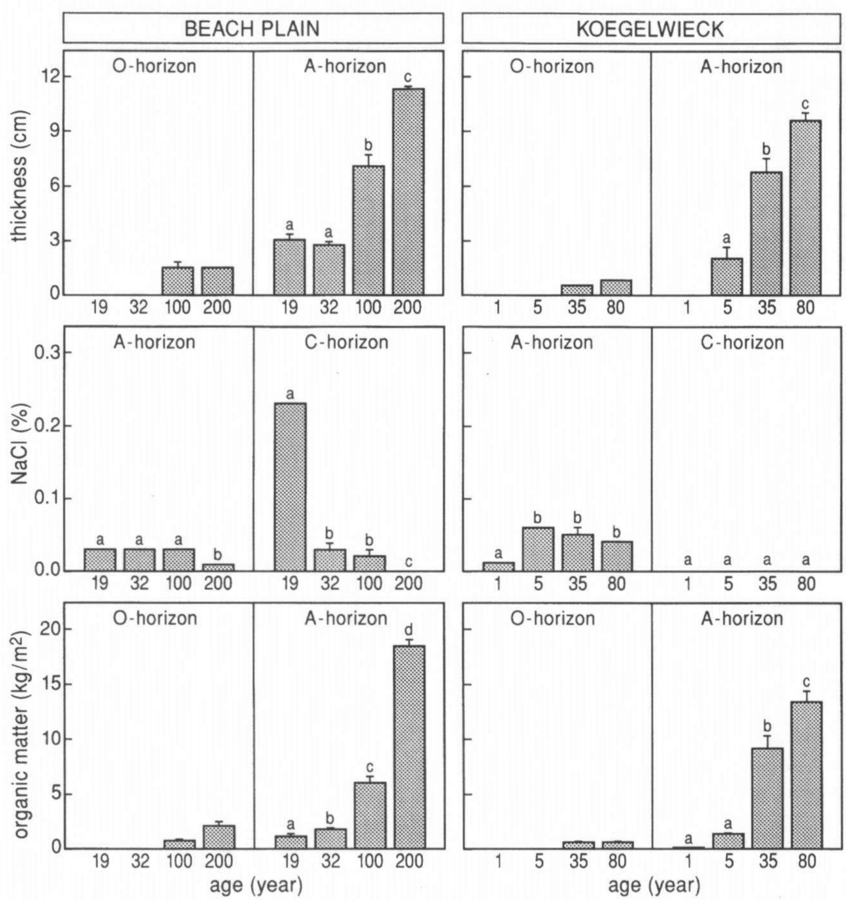

Fig. 2. The thickness, NaCl (%) and total organic matter (kg m^{-2}) in the litter (O), organic enriched mineral (A) and mineral horizon (C) of the soil sites on Schiermonnikoog (Beach plain) and Terschelling (Koegelwieck) chronosequences. Totals with the same letter within a soil horizon were not significantly different. The standard error between the samples is the vertical line on top of the totals.

the upper 20 cm (Fig. 3). The A horizon decalcified within 32 years. The A horizon of the 19-year-old site contained twice as much $CaCO_3$ as the C horizon at this site.

The amount of exchangeable bases increased slightly in the 19-year-old site till the 100-year-old site, and decreased for the 200-year-old site (Figs 3 and 4). Because the loss of $CaCO_3$ exceeded the increase in time of the amount of exchangeable bases, the total acid buffer capacity decreased with time.

In the beach plain chronosequence the $pH(H_2O)$ was significantly correlated ($P<0{\cdot}001$) with the percentage NaCl and the amount of organic matter calculated only for the A horizon (Table 2). The $CaCO_3$ and ECEC were not significantly correlated with the $pH(H_2O)$. The ECEC was significantly correlated with the sodium and magnesium saturation of the exchange complex indicating a salt dominance in the soils.

Koegelwieck sequence on Terschelling

Development of the vegetation. The soil of the 1-year-old site is sparsely vegetated with *Juncus alpinoarticulatus* ssp. *atricapillus*, *Centaurium littorale* and *Samolus valerandi*

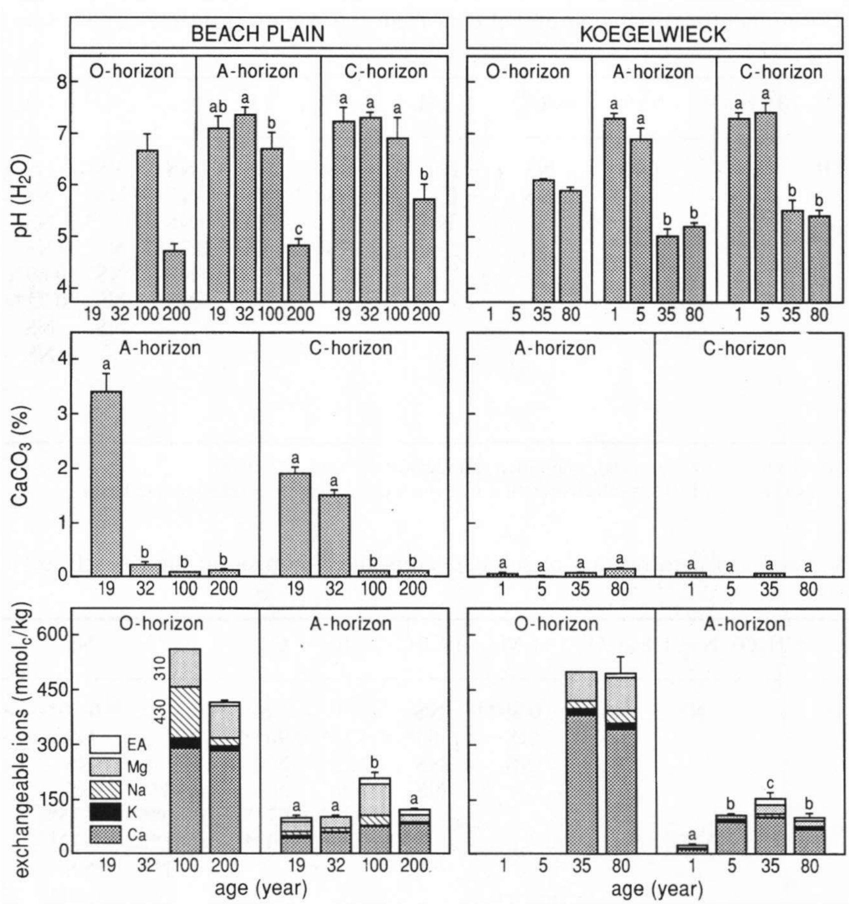

Fig. 3. The pH(H_2O), $CaCO_3$ (%), effective cation exchange capacity (mmol$_c$ kg^{-1}), exchangeable bases (mmol$_c$ kg^{-1}) and exchangeable acidity (EA) measured for three soil horizons: litter (O), organic enriched mineral (A) and mineral horizon (C) for the soil chronosequences. Totals with the same letter within a soil horizon were not significantly different. The standard error between the samples is the vertical line on top of the totals.

(Table 1). Herbaceous species, such as *Schoenus nigricans*, *Juncus alpinoarticulatus* ssp. *atricapillus*, *Centaurium littorale* and *Samolus valerandi* cover the 5-year-old site. The oldest two sites are densely vegetated with shrubs and grasses, including *Oxycoccus macrocarpos*, *Erica tetralis* and *Salix repens* (35-year-old site) and *Oxycoccus macrocarpos* and *Calamagrostis epigejos* on the 80-year-old site.

Development of soil horizons. During the soil development a dark (10 YR 2/1; black) organically enriched mineral surface horizon (A) and also on the 35- and 80-year sites an organic litter layer (O) (10 YR 3/2; very dark greyish brown) developed on the mineral subsoil (C) (2·5 Y 5/2; greyish brown). The average depth of the mineral surface horizon (A) increased and the organic litter layer (O) remained equal with age (Fig. 2).

Chemical characteristics of the soil horizons. All the sites are completely desalinized, with NaCl contents of 0·01–0·05% (Fig. 2).

Table 2. Results of a correlation of soil data from the A-horizon in the beach plain chronosequence

	$pH(H_2O)$	NaCl	$CaCO_3$	O.M.	ECEC	EB	Ca	K	Na	Mg
$pH(H_2O)$	–	– 0·83**	NS	– 0·95**	NS	NS	NS	NS	NS	NS
NaCl		–	NS	– 0.82*	NS	NS	NS	NS	NS	NS
$CaCO_3$			–	NS	NS	NS	NS	0·72*	NS	NS
O.M.				–	NS	NS	0·73*	NS	NS	NS
ECEC					–	0·97**	NS	NS	0·69*	0·92**
EB						–	NS	NS	0·71*	0·96**
Ca							–	NS	NS	NS
K								–	NS	NS
Na									–	0·83*
Mg										–

N of cases 11 (A horizon samples), one-tailed significance * – 0·01 ** – 0·001
O.M.=organic matter; ECEC=effective cation exchange capacity; EB=exchangeable bases

Table 3. Results of a correlation of soil data from the A-horizon in the Koegelwieck chronosequence

	$pH(H_2O)$	NaCl	$CaCO_3$	O.M.	ECEC	EB	Ca	K	Na	Mg
$pH(H_2O)$	–	NS	NS	– 0·89**	NS	NS	NS	– 0·83**	– 0·70*	– 0·81**
NaCl		–	NS	NS	0·85*	0·87**	0·90**	NS	NS	NS
$CaCO_3$			–	NS	NS	NS	NS	NS	NS	NS
O.M.				–	NS	NS	NS	0·83**	NS	0·68*
ECEC					–	0·99**	0·97**	0·80**	0·75*	0·86**
EB						–	0·99**	0·81**	0·72*	0·88**
Ca							–	0·71*	NS	0·79*
K								–	0·81**	0·92**
Na									–	0·83*
Mg										–

N of cases 12 (A horizon samples), one-tailed significance * – 0·01 ** – 0·001
O.M.=organic matter; ECEC=effective cation exchange capacity; EB=exchangeable bases

The 1-year-old site hardly contained organic matter (Fig. 2). After 5 years the amount of organic matter steeply increased until it reached 13·5 kg m^{-2} after 80 years. The amount of organic matter in the O horizon present at the oldest two sites was lower than the amount of organic matter in the A horizons.

In the first 5 years the $pH(H_2O)$ decreased slightly in the A and C horizon. In the 35- and 80-year-old sites the pH dropped to 5 in the A and C horizons. In these sites the pH was higher in the litter layer than in the A and the C horizons and remained around 6 (Fig. 3).

The soils of the four sites contained no measurable $CaCO_3$ (<0·1%) in the upper 20 cm (Fig. 3).

The total amount of exchangeable bases in the O horizon is almost four-fold higher than in the A horizon without significant increase after 80 years (Fig. 3). The total amount of exchangeable bases in the A horizon increased in the 5-years-old site till the 35-year-old site and decreased slightly in the 75-year-old site (Figs 3 and 4).

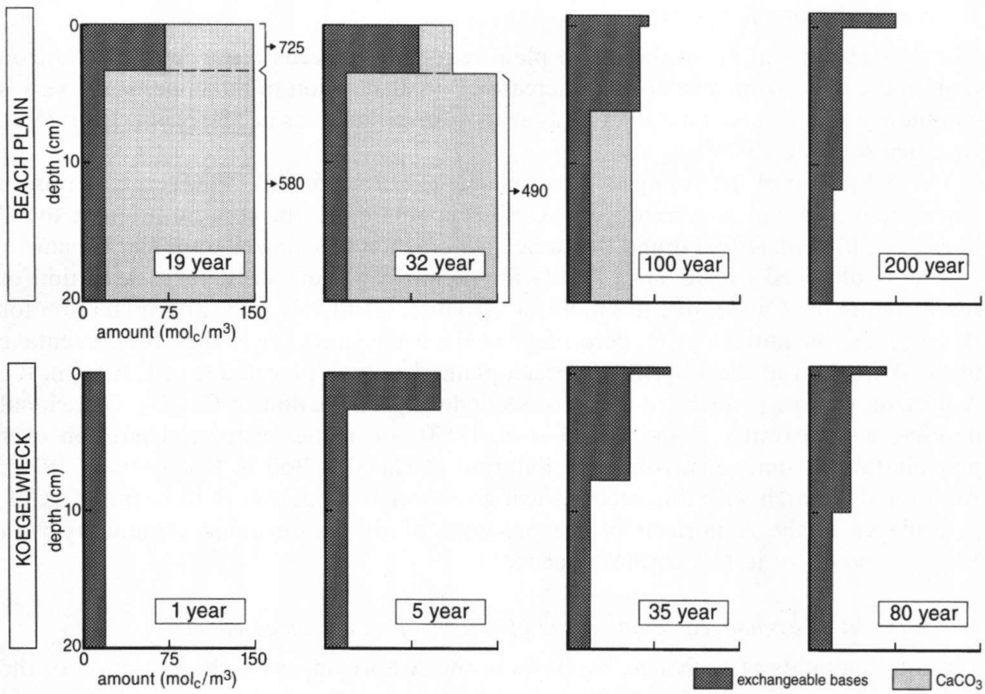

Fig. 4. The individual contribution of $CaCO_3$ and exchangeable bases to the pH buffering capacity expressed on volume basis as (mol$_c$ m^{-3}) to a maximum depth of 20 cm in the two chronosequences.

In the Koegelwieck chronosequence the pH(H_2O) was significantly correlated (P<0·001) with the amount of organic matter and exchangeable base such as K, Na and Mg in the A horizon (Table 3). The ECEC was not significantly correlated with the pH(H_2O). The ECEC is significantly correlated with the K, Na and Mg saturation of the exchange complex except for the Ca saturation.

DISCUSSION

Accumulation of organic matter

The vegetation of the beach plain has developed into a forest and that of the Koegelwieck into grasses and shrubs after 100 years. The two chronosequences differ not only in vegetation development but also in organic matter accumulation rate. The total increase of organic matter is slower in the calcareous beach plain sequence on Schiermonnikoog than in the Koegelwieck, resulting in a larger accumulation of organic matter in the Koegelwieck in the first 100 years. Invasion of the shrub *Oxycoccus macrocarpos*, with badly decomposable plant material, in the mesotrophic community with *Schoenus nigricans* and a low buffer capacity and pH of the soil stimulates the accumulation (Wilson 1960). Berendse and Olff (see Grootjans *et al.* 1995) measured a faster increase in mineralization rate with age in the calcareous beach plain chronosequence than in the Koegelwieck chronosequence, which may also explain the slower organic matter accumulation in the beach plain chronosequence.

Calcium carbonate dynamics

The decrease of $CaCO_3$ in the beach plain sequence proceeds faster in the A horizon than in the C horizon. The noticed increase of decalcification in the upper soil layers is common in areas where rainfall exceeds evapotranspiration, as in The Netherlands (Van Breemen & Protz 1988).

The A horizon of the youngest beach plain site (19 years old), however, contains an almost two-fold higher percentage of $CaCO_3$ compared to the concentration in the C horizon. Olff *et al.* (1993) found the same phenomenon in salinized dune slacks, similar to results obtained by De Vries (1961) for desalinized dune slack soils. Accretion of sand, containing $CaCO_3$ due to sandblow activities, is unlikely to be an explanation for this, because the initial $CaCO_3$ percentage of the soil is much lower than the percentage in the A horizon of the 19-year-old beach plain. The high percentage of $CaCO_3$ in the A horizon is most probably a result of secondary precipitation of $CaCO_3$. Occasional flooding with seawater (Van Tooren *et al.* 1983) and higher evapotranspiration over precipitation in summer favours precipitation of $CaCO_3$ (Bolt & Bruggenwert 1978). Additional research with thin sections will give more information of these high $CaCO_3$ percentages in the A horizon of the pre-stage of the mesotrophic community with *Schoenus nigricans* in this chronosequence.

Development of exchangeable bases and effective cation exchange capacity

The total amounts of exchangeable bases in the A horizons, with the exception of the 100-year-old beach plain and 35-year-old Koegelwieck site, are not significantly different in the beach plain to those in the Koegelwieck sites. The amount of Ca is not only due to supply of Ca from the $CaCO_3$ but also to additions during flooding in winter and early spring. The amount of Mg and Na on the exchange complex also increase during groundwater flooding.

Except for the two oldest sites of both chronosequences, the ECEC of the A horizons increase with time and are most probably related to increasing organic matter content (Leinweber *et al.* 1993). The decrease of the ECEC in the two oldest sites is somewhat puzzling. Helling *et al.* (1964) described a decrease in the dissociation of functional ion exchange sites of the organic matter with decreasing pH, explaining the lower values of the two oldest sites.

Buffer ranges in relation to pH

The pH of the A horizon in all the younger sites is around 7, indicating that the soils are buffered by calcium carbonate (Bruggenwert *et al.* 1991). Except for the youngest beach plain site, the amount of $CaCO_3$ is negligible in the A horizons of both chronosequences. In the beach plain sequence the pH in the A horizon of the mesotrophic community with *Schoenus nigricans* is probably buffered by brackish surface water, considering the positive correlation with NaCl and the high proportion of Na and Mg on the exchange complex. The pH of the youngest sites in the (freshwater) Koegelwieck chronosequence appears to be buffered around 7 by the exchange complex with a high base saturation; the cation exchange rate (Bruggenwert *et al.* 1991). These bases predominantly originate from base-rich groundwater discharged in the valley from deeper calcareous layers (Grootjans *et al.* 1995). In general, the total cation exchange complex in dune slack soils is positively related to the amount of organic matter (Leinweber *et al.* 1993). This holds true for the mesotrophic *Schoenus nigricans* community (5 years) of the Koegelwieck chronosequence, but not for the youngest site (1 year), which has no measurable amount of organic matter and therefore a low ECEC. The high pH of this site is probably best explained by the absence of strong acidifying mineralization products and by flooding of groundwater during winter and early spring.

Persistence of the mesotrophic basiphilous species

The habitat conditions of the mesotrophic community with *Schoenus nigricans* and its associated rare species are remarkably similar in the two chronosequences, but their time of establishment and persistence is very different. The A horizon appears to be characterized by a pH above 6·5, a low amount of organic matter and $CaCO_3$, a high base saturation and a very low percentage of NaCl. This is in agreement with results from other dune slacks (De Vries 1961; Sparling 1968; Schat 1982).

The relationship between $CaCO_3$ and *Schoenus nigricans* stands in our dune slacks is somewhat puzzling. In the beach plain sequence much $CaCO_3$ is present in the C horizon, within the rooting zone, so acidification of this zone will not be a problem for decades (De Vries 1961). In the Koegelwieck, however, a mesotrophic *Schoenus nigricans* community is present on deeply decalcified soils (up to 1·5 m) (Grootjans *et al.* 1995). The high pH measured here is probably the result of a temporary through-flow or base-rich groundwater during flooding, which increases the exchangeable base of the exchange complex *and* buffers the acid input from natural and anthropogenic sources. Nevertheless, the community rapidly declines with an increase of organic matter above *c.* 7% (Lammerts *et al.* 1995). At these high levels of organic matter the cation exchange mechanism cannot counterbalance the acid input without the annual groundwater addition.

In the beach plain sequence the situation is different. The pH decreases markedly in the very old stages of succession. The basiphilous plant community in the initially brackish calcareous beach plain (*c.* 20–25 years) persists for almost twice as long as in the Koegelwieck (Grootjans *et al.* 1995). This is associated with a much slower increase of organic matter and a high acid buffering capacity as compared to the Koegelwieck sequence, which is capable of neutralizing higher amounts of acids. But after several decades the increased pool of nutrients in the organically enriched mineral layer facilitates fast-growing species, which replace *Schoenus nigricans* and many associated rare species.

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