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Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea

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Abstract. Salt marsh development on the coastal barrier island of Schiermonnikoog (The Netherlands) was compared with two other salt marsh systems in the Wadden Sea. Accretion rate, nitrogen accumulation and changes in plant species composition were investigated using chronosequences. The age of the marsh was estimated from aerial photographs and old maps. In 7230 plots, the elevation of the marsh surface, the thickness of the sediment layer (clay) and the presence of plant species was recorded. In addition, the nitrogen pool was measured at each successional stage.

Accretion rates were similar in the three salt marshes. Higher accretion rates were found at younger marshes. A strong linear relationship between nitrogen pool size and thickness of the clay layer was found for the three marshes. The accumulation rate of nitrogen is therefore strongly related to the accretion rate. Thus, more nitrogen is present in the sediment of later successional stages where more clay has accumulated. On the high salt marsh (55 cm + MHT),*Armeria maritima* disappeared and *Artemisia maritima*, *Juncus gerardi* and *Elymus athericus* established at sites with a thicker clay layer. On the low salt marsh (25 cm +MHT), *Plantago maritima*, *Puccinellia maritima* and *Limonium vulgare* disappeared and *Atriplex* (*Halimione*) *portulacoides* established. Apparently, with the accumulation of clay and therefore of nitrogen, tall growing species take over in salt marshes not grazed by livestock.

Keywords: Accretion rate; Sea level rise; Species response curve; Succession.

Nomenclature: van der Meijden et al. (1990).

Introduction

This study was set up in order to detect a general pattern of development of coastal barrier salt marshes in the Wadden Sea. Salt marsh development on several coastal barrier islands in the Wadden Sea has been described previously (Jensen 1985; Roozen & Westhoff 1985; Bakker et al. 1993; Olff et al. 1997). Accumulation of nitrogen over time has been found to be a possible mechanism causing vegetation succession on salt marshes (Olff et al. in press). Most of the nitrogen which enters the salt marsh is located in clay material which is deposited on the marsh due to flooding of seawater. The rate of clay accretion is therefore important for the rate of vegetation succession. Accretion rates are relatively low in salt marshes on coastal barrier islands, compared to salt marshes on the mainland (Dijkema et al. 1990). A relatively thin layer of fine-grained sediment (clay) is found on these marshes, which occurs usually at low elevations, due to a higher inundation frequency, but it is also found on older marshes where sediment deposition has taken place for a longer period of time. The amount of nitrogen in the topsoil is strongly related to the thickness of the clay layer (Olff et al. in press). Accordingly, only a relatively small amount of nitrogen can be expected in the sediments of coastal barrier salt marshes. This could explain the fact that plant production in many salt marshes has been found to be limited by nitrogen (Tyler 1967; Jefferies & Perkins 1977; Jensen et al. 1986; Kiehl et al. 1997).

It is generally accepted that the zonation pattern of vegetation along an elevation gradient on coastal barrier salt marshes does not reflect succession (Roozen & Westhoff 1985; de Leeuw et al. 1993). This is because the elevational difference along this gradient was already present at the time when the salt marsh development started. Changes in plant species composition over time, however, can be investigated using chronosequences. By comparing several successional stages, the course of succession can be deduced. This was done for the coastal barrier island of Schiermonnikoog, The Netherlands by Olff et al. (in press), who found that *Elymus athericus* became dominant over a large vertical range in the marsh after 200 yr of succession.

This study compares three salt marsh systems in the Wadden Sea which are not grazed by cattle, in order to generalize the salt marsh development which was described for Schiermonnikoog by Olff et al. (in press). First, the rate of clay and nitrogen accumulation will be described for these marshes separately. Secondly, an attempt will be made to extrapolate the linear relationship between the nitrogen pool and the thickness of the clay layer found on Schiermonnikoog. Finally, the response of plant species to changes in the thickness of the clay layer will be compared for the three salt marshes.

Methods

Study area

Salt marshes that have not been grazed by cattle are rare in the Wadden Sea (Bakker 1983). Only a part of the salt marsh at the peninsula of Skallingen, Denmark (55°30' N, 8 °20'E), the Boschplaat at the coastal barrier island of Terschelling, The Netherlands (53°26'N, 5°28'E) and the Oosterkw elder on the coastal barrier island of Schiermonnikoog, The Netherlands (53°30'N, 6°10'E) are known to have been ungrazed in recent years. These areas have been studied in this paper (Fig. 1). Mean tidal amplitude varies between the three study areas and the effects of this difference were removed by calculating the relationship between marsh surface elevation (relative to N.A.P. = Dutch Ordnance Level) and inundation frequency.

The development of the Skallingen salt marsh started at the beginning of this century in the shelter of a dune ridge (Jacobsen 1952). During its development, some areas of the marsh were washed away by the North Sea, resulting in rejuvenation. The age of the marsh was estimated from aerial photographs and maps and the date at which vegetation became established was used as an indication of the first stages of salt marsh development. The age of the Skallingen salt marsh varies between 70 and 100 yr, with the sheltered northern section probably being the oldest part of the system. A large part of the salt marsh is grazed by cattle, but the salt marsh near the tidal flats is fenced and ungrazed. Mean tidal amplitude is 1.5 m and the Mean High Tide level (MHT) is ca. 67cm above N.A.P. level (Jensen et al. 1985).

The Boschplaat has developed in the shelter of an artificial sand dike which was established in 1931 (Roozen & Westhoff 1985; Westhoff & van Oosten 1991); this indicates an age of > 60 yr. A small area known as ÔDe Gri‘Õ is thought to be much older: 500 yr (Westhoff & van Oosten 1991); it is presently subjected to cattle grazing. The age of this marsh makes it an interesting area and therefore the data on clay accumulation are presented in this paper. However, the area is grazed by cattle and therefore it is not included in the vegetation analysis. Mean tidal amplitude at the Boschplaat is ca.2m and the MHT level is 87cm + N.A.P.

An artificial sand dike in the western part and natural dunes in the eastern part of the Oosterkwelder on Schiermonnikoog protect the salt marsh from the influence of the North Sea. New dunes are still being formed in the eastern part. As a result, the salt marsh has extended to the east during the past 200 yr (Bakker 1989; Olff et al. 1997) resulting in a well-developed local chronosequence. Salt marsh age ranges from 200 yr in the extreme west to 100, 65, 35, 25 and 10 yr towards the east. Mean tidal amplitude amounts to approximately 2.3 m and the MHT level is 100 cm above N.A.P.

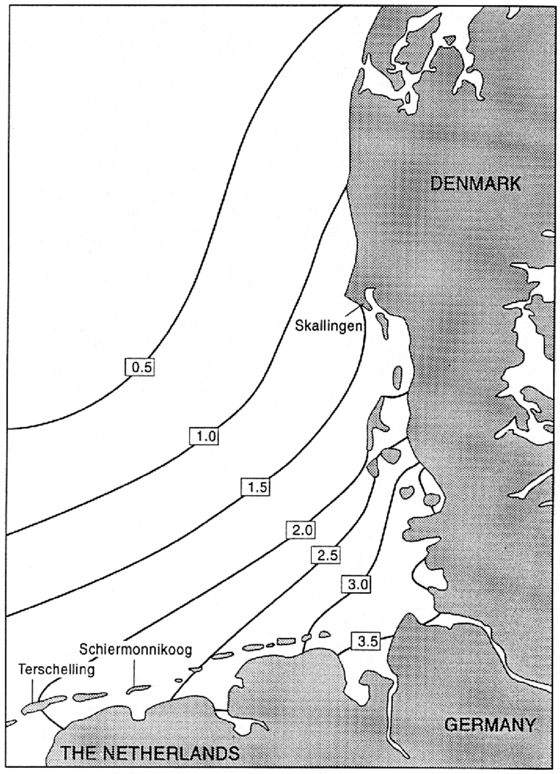

Fig.1. Location of the study sites: Terschelling, Schiermonnikoog and Skallingen. Isolines of tidal amplitude (m) are indicated.

Transects

Salt marsh system parameters were described by the establishment of transects which were approximately 10 m $\times$50 m in size. Six transects were established on the island of Schiermonnikoog, five on the island of Terschelling and three on the peninsula of Skallingen. To cover the vegetation zonation along the geomorphological gradient, each transect was established from a dune to the low salt marsh. The longest side of each transect ran perpendicular to the contour lines of a dune. The transects were divided into plots of 1m ^{2}. In total, 7230 squares of 1m ^{2} were used (Table 1). In each square, surface elevation according to N.A.P. and the thickness of the clay layer was measured. In addition, the presence of all plant species was recorded.

Tidal inundation

Data for mean high water levels and inundation frequencies were obtained from Rijkswaterstaat, the Dutch State Water Works, and the harbour of Esbjerg, Denmark. The relationship between the inundation frequency and the elevation of the marsh surface was calculated by fitting a non-linear regression curve for the three areas separately. The following model was used (Olff et al. in press):

$$I = 706/(1+\exp(A*(E - M))), \quad (1)$$

where I=inundation frequency; A = a constant (5.6 for Schiermonnikoog and Skallingen, 4.6 for Terschelling); E = elevation of the marsh surface; M = MHT-level.

Clay accretion and nitrogen pool

The thickness of the clay layer was analyzed separately for each successional stage and was related to the base elevation (elevation of the sandy substrate underneath the clay layer). In this case, the base elevation was used instead of the elevation of the marsh surface to avoid differences in the frequency of inundation due to clay accumulation. For each elevation class of 10cm, the mean clay thickness was calculated. Accretion rates were then calculated by dividing the thickness of the clay layer per elevation class by the age of the marsh.

On three sites along each transect on Terschelling and Skallingen (high, mid and low salt marsh), and two sites along each transect on Schiermonnikoog (high and low salt marsh), sediment samples were taken at three depths: 0-10 cm, 10-25 cm and 25-50 cm. When the border between the sandy sublayer and the clay layer fell within these classes, the class was subdivided and samples were taken in both subclasses. The total nitrogen content of sediment samples was analyzed using the modified Kjeldahl procedure of Wieniger (1936). Volumetric sediment samples to measure bulk density were taken at the same depths as the nitrogen samples. The total nitrogen pool in the sediment was calculated by multiplying nitrogen content by bulk density. Values for each depth range were then added to give a total value for the uppermost 50 cm of sediment. The total nitrogen pool in the sediment was calculated for 36 sites (12 sites on Schiermonnikoog, 15 on Terschelling and nine on Skallingen). A standardized depth of 50 cm was used at all sites in order to calculate the total nitrogen pool for a fixed volume of sediment from which plants can extract nitrogen.

The 500-yr old marsh on Terschelling was not used in the regression analysis because grazing by cattle has probably caused a reduction in the thickness of the clay layer due to trampling. Using the regression coefficient and the calculated accretion rates, nitrogen accumulation rates in the marsh were assessed.

Species distribution

A second order response surface with linear interaction was calculated for each plant species, where the elevation of the marsh surface and the thickness of the clay layer were two independent parameters. The probability (P) for a species to be present, after logit transformation of the dependent variable, is given by:

$$P=1/(1+\exp(a_1C + a_2E+a_3C^2+a_4E^2+a_5CE+a_6)) \quad (2)$$

where a_1 to a_6 are the parameters of the model, C = the thickness of the clay layer and E = the elevation of the marsh surface (+MHT). Each parameter was tested for entry in a forward stepwise multiple regression analysis (Huisman et al. 1993). The parameters for each species are given in App.1, and the model characteristics in App.2. The probability P was calculated for two marsh surface elevations (25 and 55 cm +MHT). In this way, response curves for each species were calculated with clay thickness as an independent parameter. When a species occurred in one transect only, it was omitted from the analysis. Important for the interpretation of the curves is that the tidal influence is not changing when clay accumulates. Each curve, therefore, shows the response of a species to changes in the thickness of the clay layer at a constant elevation level for the three salt marshes.

Results

The main differences in inundation frequency between Schiermonnikoog, Terschelling and Skallingen are due to the differences in MHT-level (Fig. 2). At MHT-level, the inundation frequency amounts to ca. 300 floodings per year. In order to exclude differences

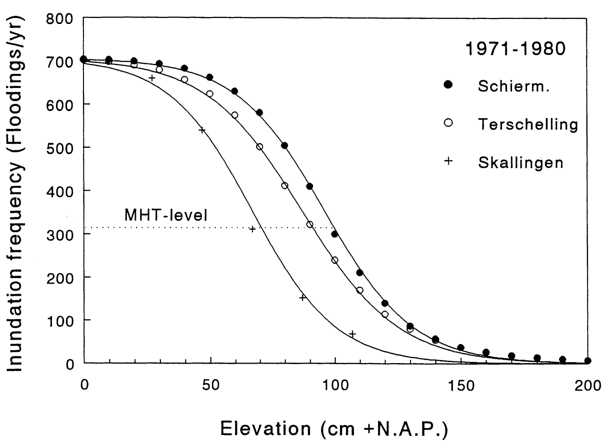

Fig. 2. Inundation frequency as a function of salt marsh surface elevation (above N.A.P.) for the period 1971-1980 at Schiermonnikoog, Terschelling and Skallingen.

between the areas which are a result of tidal regime, the elevation of the marsh surface above MHT-level is used to compare the various salt marshes in the Wadden Sea.

The relationship between the thickness of the clay layer and the nitrogen pool for Schiermonnikoog, Terschelling and Skallingen (Fig.3) is described by:

Y=19 X + 125 (n=33; r=0.91, p< 0.001) (3)

The three open circles with brackets indicate the 500-yr old marsh on Terschelling. These points were not used in the analysis since this marsh is now grazed by cattle and trampling might have decreased the thickness of the clay layer considerably. The regression coefficient gives the nitrogen accumulation rate: 19 g N$m^{-2}cm^{-1}$clay. In bare sand, the sediment contains 125 g N/m^2 to a depth of 50 cm, whereas a salt marsh with 30 cm of clay contains 695 g N/m^2 in the same volume of sediment.

An almost linear decrease in the thickness of the clay layer was found from a low to a high marsh (Fig. 4). For Schiermonnikoog, the thickness of the clay layer in the low marsh ranged from 2 cm after 10 yr of succession to 16 cm after 200 yr of succession. On Terschelling, the transects of 50 and 60 yr revealed a clay layer that ranged from 11 cm to 25 cm at the lowest marsh sites. The salt marsh of 500 yr had accumulated a clay layer of 32 cm at an elevation between 30 and 40 cm +MHT. On Skallingen, the salt marshes of 70 and 80 yr were relatively similar; they had accumulated 15 cm of clay on the lowest sites. The salt marsh of 100 yr had accumulated more clay on the high marsh sites but was similar to the other marshes at a lower elevation.

The highest clay accretion rates were found on Schiermonnikoog in the 25-yr old marsh, where the maximum accretion rate amounted to 3.4 mm/yr at a base elevation of 20-30 cm +MHT (Fig. 5). After 25 yr

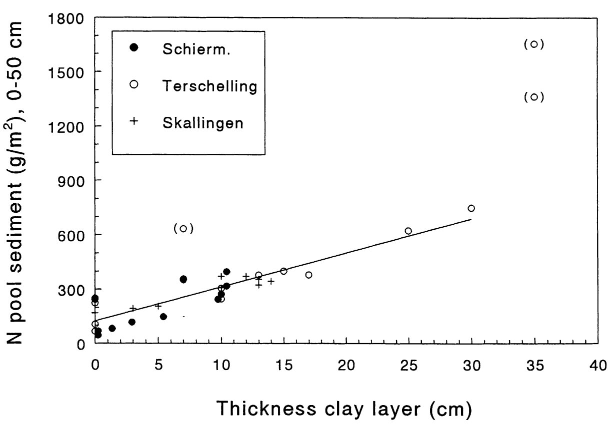

Fig. 3. The relationship between the thickness of the clay layer and sediment nitrogen pool size (0-50 cm depth) based on samples collected from Schiermonnikoog, Terschelling and Skallingen.

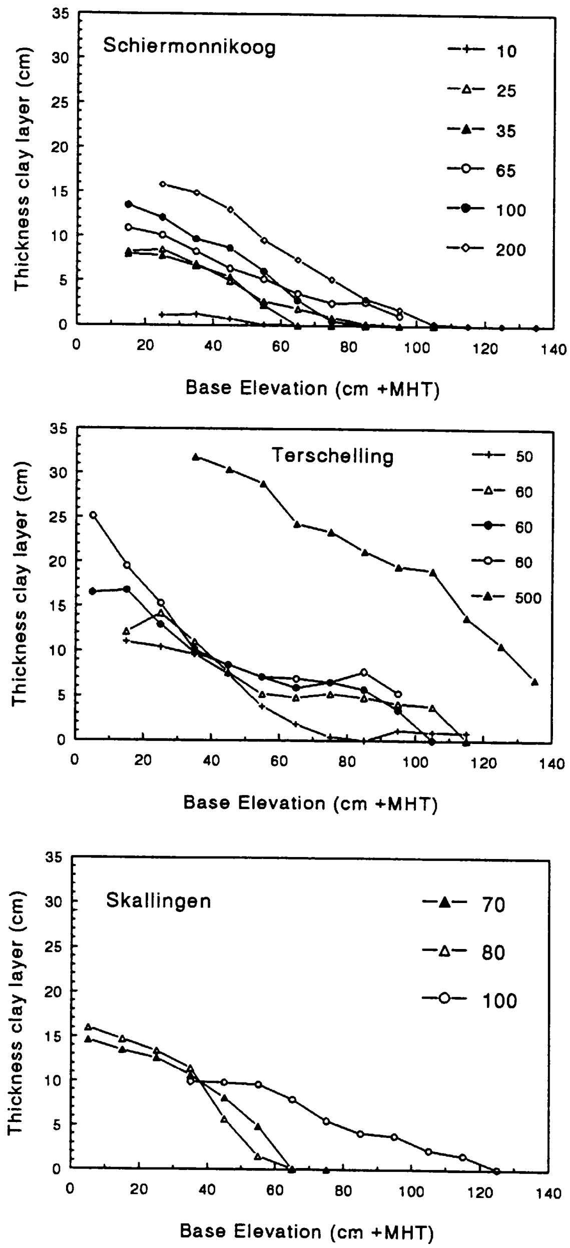

Fig. 4. Relationship between clay layer thickness and base elevation for Schiermonnikoog, Terschelling and Skallingen. The numbers in the graph indicate the successional stage (yr) of the marsh.

of salt marsh development, the accretion rates decreased. At higher elevations accretion rates were lower, especially on younger salt marshes. Accretion rates on Terschelling and Skallingen were similar to those on Schiermonnikoog. Nitrogen accumulation rates were low on older marshes: 1 g N $m^{-2}yr^{-1}$ for a 500-yr old salt marsh. No difference was found for this marsh between the elevation classes. For the 25-yr old marsh the rate was higher than at the other stages while it

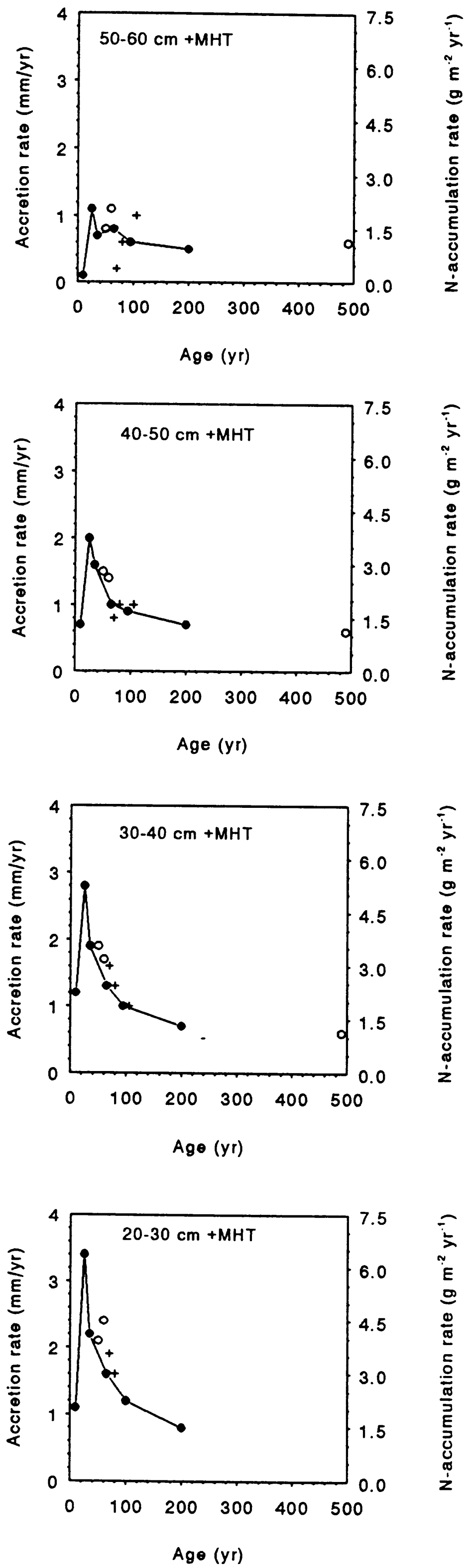

Fig. 5. Clay accretion and nitrogen accumulation rates over time for four base elevation classes at Schiermonnikoog (●), Terschelling (○) and Skallingen (+). Open circles between brackets represent a 500-yr stage on Terschelling which was not used in the regression analysis.

increased towards the low marsh, from 2 g N m^{-2} yr^{-1} in the high marsh (50 - 60 cm +MHT) to 6.5 g N m^{-2} yr^{-1} in the low marsh (20-30 cm +MHT). The very young marsh of 10 yr showed low accretion and N-accumulation rates.

The species responses to changes in the clay thickness were not exactly similar in the three salt marshes (Figs. 6 and 7). The type of response for most species was however comparable. The length of each curve indicates the range for which data existed. In the high marsh of 55 cm +MHT, *Armeria maritima* was present with low frequency at the sandy stages and disappeared when clay accumulated. *Festuca rubra* and *Juncus gerardi* were mostly present at intermediate stages, although *Festuca rubra* had a probability of > 70 % of being present in all marshes. *Artemisia maritima* and *Elymus athericus* were more frequent at stages with a thicker clay layer present. *Artemisia maritima* and *Juncus gerardi* were present more often on Schiermonnikoog and Skallingen than on Terschelling. The response of *Artemisia maritima* on Skallingen was different from Terschelling and Schiermonnikoog and the probability of being present declined. On the low marsh, *Plantago maritima*, *Puccinellia maritima* and *Limonium vulgare* were present at the sandy sites. *Atriplex* (*Halimione*) *portulacoides* was always present at sites with a thick clay layer. Differences between the three marshes were not pronounced in the low marsh. *Plantago maritima* was present at a low frequency and *Puccinellia maritima* showed a different response on Skallingen.

Discussion

Accretion rates

The accretion rates in the three Wadden Sea salt marshes appeared to be very similar. The maximal accretion rates occurred in younger marshes at a base elevation between 20 and 30 cm +MHT and amounted to ca. 3.4 mm/yr for a 25-yr old salt marsh. Since there were only a few plots available below this elevation, no accretion rates could be calculated for the base elevation between 0 and 20 cm +MHT. According to Dijkema et al. (1990), the highest accretion rates can be found between 0 and 20 cm +MHT. Therefore, maximal accretion rates in these salt marshes will probably be higher than 3.4 mm/yr. Roozen & Westhoff (1985) reported similar rates for Terschelling. The lower accretion rates in older marshes were probably due to shrinkage of the clay layer by a decrease in water content. This process is often irreversible (de Glopper 1989) and could be important at sites with a thick clay layer. Another possibility is that an increase in marsh elevation caused a decrease in

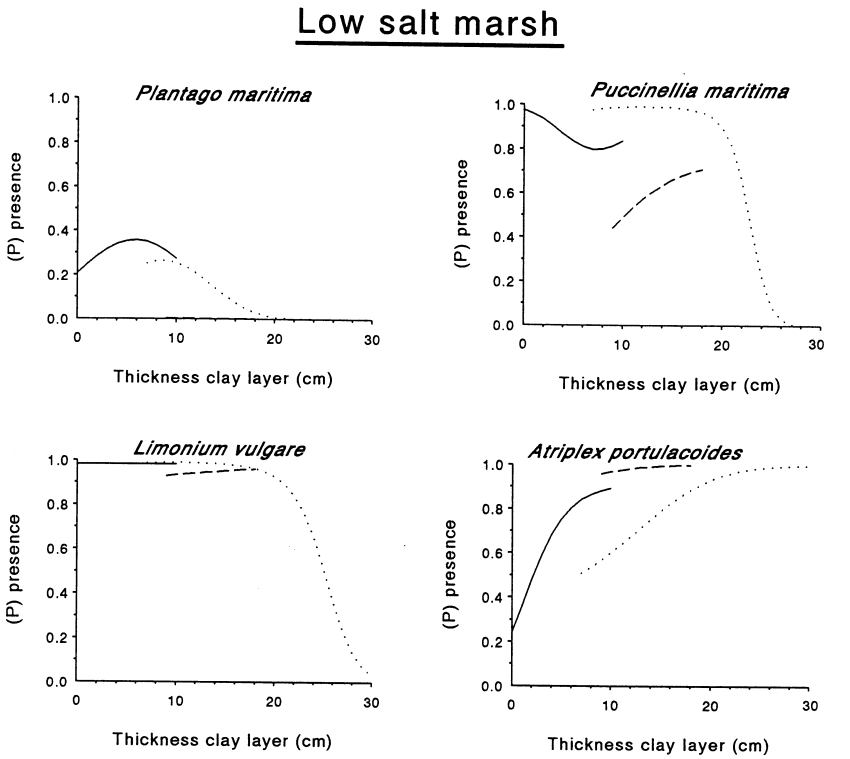

Fig. 6. Species response curves for a low salt marsh (25 cm +MHT) in relation to the thickness of the clay layer. (—–) Schiermonnikoog; (······) Terschelling; (Ñ Ñ) Skallingen.

the number of flooding events which resulted in a decrease of the accretion rate. Pethick (1981) also found a high accretion rate in younger salt marshes. He did not find any further increase in elevation after 200 yr of salt marsh development. With a continuous rise in high water level, this is not likely to happen in the Wadden Sea.

A highly correlated linear relationship was found between thickness of the clay layer and the N-pool for the three salt marsh areas allowing the calculation of a nitrogen accumulation rate of 19gN/m ^{2}/cm of clay. This is lower than the 43g N found by Olff et al. (in press) and the 40 g N reported by Leendertse (1995). Olff et al. (in press) extrapolated their nitrogen values from the upper layers to the deeper sediment layers. However, this extrapolation gives an overestimation of the measured nitrogen values, especially at sites with a thick layer of clay.

Vegetation development

Elymus athericus and *Artemisia maritima* increase considerably in frequency on high marshes of Schiermonnikoog and Terschelling with a relatively thick clay layer. On Skallingen, *E. athericus* is very sparse; it was found in one transect only. An explanation for this might be that Skallingen is located at the edge of the geographical range of this species (Clapham et al. 1962). The presence of *E. athericus* and *A. maritima* on Schiermonnikoog and Terschelling is in agreement with results from Roozen & Westhoff (1985) and Leendertse (1995) on Terschelling, who reported the dominance of *E. athericus* in permanent plots in a later successional phase, at sites with a high nutrient status. Similarly, they found that *Atriplex portulacoides* became dominant at later successional stages on a low marsh in combination with a clay layer of 15 cm.

An increase of nitrogen in a nitrogen-limited system will not only increase plant productivity, but may also increase the salt tolerance of plants (Stewart et al. 1979; Jensen 1985; Rozema et al. 1985). Chenopods like *Atriplex portulacoides* will be able to tolerate more salt if more nitrogen is present and the sediment is well aerated (Jensen 1985; Roozen & Westhoff 1985). Plants can produce more nitrogen-containing osmotica like proline and betaine when more nitrogen is present. Examples are *Elymus athericus* and *Atriplex portulacoides*, which both accumulate methylated quaternary ammonium compounds (MQAC) for osmoregulation and were found to become established in marshes with high nitrogen levels (Stewart et al. 1979). *Plantago maritima* and *Juncus gerardi* do not accumulate nitrogen compounds for osmoregulation (Stewart et al. 1979) and therefore are not expected to

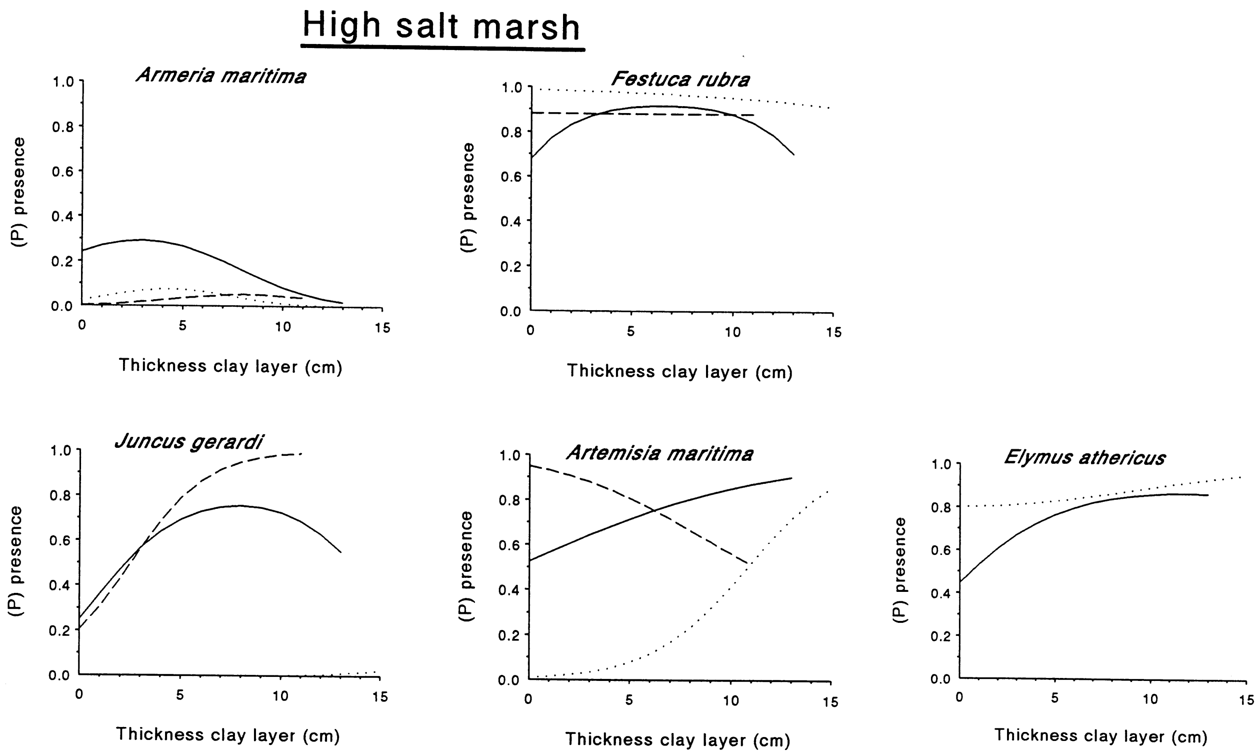

Fig. 7. Species response curves for a high salt marsh (55 cm +MHT) in relation to the thickness of the clay layer. (—–) Schiermonnikoog; (······) Terschelling; (Ñ Ñ) Skallingen.

compete successfully with other species when the marsh becomes older. Moreover, they may be outcompeted by light interception by the taller *E. athericus* and *A. portulacoides*.

In conclusion, clay and total nitrogen accumulation rates are very similar among the three Wadden Sea salt marsh systems. In these marshes *Artemisia maritima*, *Atriplex portulacoides* and *Elymus athericus* become established at sites with a thick clay layer. Tall growing species such as *E. athericus*, *A. portulacoides* and *A. maritima* are expected to compete successfully with other species when nitrogen availability is high. Eventually these marshes will become species-poor communities at higher nitrogen levels, as long as they are not grazed by large herbivores.

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References

Bakker, J.P. 1983. Use and management of salt marshes on sand-dune islands. In: Wolff, W.J. (ed.) *Ecology of the Wadden Sea*, pp. 9/290-302. A.A. Balkema, Rotterdam.

Bakker, J.P. 1989. *Nature management by grazing and cutting.* Kluwer, Dordrecht.

Bakker, J.P., de Leeuw, J., Dijkema, K.S., Leendertse, P.C., Prins, H.H.T. & Rozema, J. 1993. Salt marshes along the coast of The Netherlands. *Hydrobiologia* 265: 73-96.

Clapham, A.R., Tutin, T.G. & Warburg, E.F. 1962. *Flora of the British Isles.* 2nd ed. Cambridge University Press, London.

de Glopper, R.J. 1989. *Land subsidence and soil ripening.* Flevobericht 306, Rijkswaterstaat directie Flevoland, Lelystad.

de Leeuw, J., de Munck, W., Olff, H. & Bakker, J.P. 1993. Does zonation reflect the succession of salt marsh vegetation? A comparison of an estuarine and a coastal bar island marsh in The Netherlands. *Acta Bot. Neerl.* 42: 435-446.

Dijkema, K.S., Bossinade, P., Bouwman, P. & de Glopper, R.J. 1990. Salt marshes in The Netherlands Wadden Sea: rising high-tide levels and accretion enhancement. In: Beukema, J.J., Wolff, W.J. & Brouns, J.J.W. (eds.) *Expected effects of climatic change on marine coastal ecosystems,* pp. 173-188. Kluwer Academic Publishers, Dordrecht.

Huisman, J., Olff, H. & Fresco, L.F.M. 1993. A hierarchical set of models for species response analysis. *J. Veg. Sci.* 4:

37-46.

Jacobsen, B. 1952. Landskabsudviklingen i Skallingenmarsken. *Geogr. Tidsskr.* 52: 147-159.

Jefferies, R.L. & Perkins, N. 1977. The effects on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk. *J. Ecol.* 65: 867-882.

Jensen, A. 1985. On the ecophysiology of *Halimione portulacoides*. *Vegetatio* 61: 231-240.

Jensen, A., Henriksen, K. & Rasmussen, M.B. 1985. The distribution and interconversion of ammonium and nitrate in the Skallingen salt marsh and their exchange with the adjacent coastal water. *Vegetatio* 62: 357-366.

Jensen, A., Blicher, G., Og, M. & Skovhus, K. 1986. *Kunstgodning marsk-og strandeng*. Teknikerrapport nr. 30, Botanisk Institut, •rhus Universitet.

Leendertse, P.C. 1995. *Impact of nutrients and heavy metals on salt marsh vegetation in the Wadden Sea*. Doctoral Thesis, Free University, Amsterdam.

Kiehl, K., Esselink, P. & Bakker, J.P. In press. Nutrient limitation and plant-species composition in temperate salt marshes. *Oecologia* (*Berl*.).

Olff, H., de Leeuw, J., Bakker, J.P., Platerink, R.J. & van Wijnen, H.J. In press. Vegetation succession and herbivory on a salt marsh. *J. Ecol.*

Pethick, J.S. 1981. Long term accretion rates on tidal salt marshes. *J. Sedimentol. Petrol*. 51: 571-577.

Roozen, A.J.M. & Westhoff, V. 1985. A study on long term salt marsh succession using permanent plots. *Vegetatio* 61: 23-32.

Rozema, J., Bijwaard, P., Prast, G. & Broekman, R. 1985. Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio* 62: 499-521.

Stewart, G.R., Larher, F., Ahmad, I. & Lee, J.A. 1979. Nitrogen metabolism and salt tolerance in higher plant halophytes. In: Jefferies, R.L. & Davy, A.J. (eds): *Ecological processes in coastal environments*, pp. 211-241. Blackwell, Oxford.

Tyler, G. 1967. On the effect of phosphorus and nitrogen, supplied to baltic shore meadow vegetation. *Bot. Not.* 120: 433-447.

van der Meijden, R., Weeda, E.J., Holverda, W.J. & Hovenkamp, P.H. 1990. *Flora van Nederland*. 21th ed. Wolters-Noordhoff, Groningen.

Westhoff, V. & van Oosten, M.F. 1991. *De plantengroei van de Waddeneilanden*. Stichting KNNV, Utrecht.

Wieniger, F.M. 1936. Nachtrag zur Schnellstickstoffbestimmungsmethode mit Silen als Beschleuniger. *Wochenschr. Brauerei* 53: 251-252.

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App. 1. Model parameters of the logistic species response surfaces for the dependence of the probability of occurrence on the thickness of the clay layer and the elevation of the marsh surface.

	Schiermonnikoog						Terschelling						Skallingen					
	a_1	a_2	a_3	a_4	a_5	a_6	a_1	a_2	a_3	a_4	a_5	a_6	a_1	a_2	a_3	a_4	a_5	a_6
Armeria maritima	Ð1.33	Ð0.35	0.03	0.0021	0.021	14.04	Ð0.50	Ð0.05	0.057	-	-	6.33	Ð0.65	Ð0.14	0.04	-	-	13.23
Artemisia maritima	Ð0.71	Ð0.18	-	0.0010	0.010	6.95	-	Ð0.21	-	0.0013	Ð0.01	12.44	-	Ð0.18	Ð0.01	0.001	0.01	2.87
Atriplex portulacoides	Ð0.93	-	0.03	Ð0.0001	0.014	1.20	-	0.10	Ð0.007	Ð0.0008	-	Ð1.61	-	-	-0.01	0.001	-	Ð2.18
Elymus athericus	-	Ð0.34	0.01	0.0018	Ð0.006	13.57	-	Ð0.48	Ð0.007	0.0024	-	17.85	-	-	-	-	-	-
Festuca rubra	Ð1.35	Ð0.46	0.04	0.0028	0.015	15.97	-	Ð0.43	-	0.0030	0.003	10.39	-	-	-	0.001	0.01	1.63
Juncus gerardi	Ð1.86	Ð0.81	0.04	0.0068	0.024	25.34	-	Ð0.98	0.070	0.0192	Ð0.043	19.34	0.41	Ð0.17	-	0.002	Ð0.02	4.81
Limonium vulgare	-	0.17	-	Ð0.0008	-	Ð7.93	Ð0.37	0.29	0.019	Ð0.0017	-	Ð8.99	-	0.10	-	-	Ð0.01	Ð4.50
Plantago maritima	Ð0.26	Ð0.09	0.02	0.0005	-	3.18	-	0.13	0.028	0.0006	Ð0.019	Ð0.63	-	-	-	0.001	Ð0.02	7.72
Puccinellia maritima	0.42	Ð0.28	Ð0.04	0.0052	0.009	Ð0.13	Ð1.07	0.63	0.044	Ð0.0042	-	Ð11.49	Ð0.35	-	0.01	-	-	2.73
Triglochin maritima	Ð0.36	-	-	-	-	3.92	Ð2.17	Ð0.93	0.046	0.0117	0.020	28.64	-	0.13	0.05	-	Ð0.02	Ð0.80

App. 2. Model characteristics of the logistic species response surfaces. The model χ^2 tests the null hypothesis that the parameters of the model, except for the constant, are 0. In addition, the degrees of freedom (df) and the percentage of correctly classified cases by the model (%c) are given. All values significant at $p < 0.001$.

	Schiermonnikoog			Terschelling			Skallingen		
	χ^2	df	%c	χ^2	df	%c	χ^2	df	%c
Armeria maritima	351.9	5	85	193.4	3	96	673.0	3	94
Artemisia maritima	715.0	4	76	383.9	3	86	92.7	4	68
Atriplex portulacoides	489.2	4	64	546.1	3	72	355.2	2	92
Elymus athericus	1593.7	4	79	1230.0	3	83	-	-	-
Festuca rubra	1236.4	5	79	1057.3	3	87	484.6	1	77
Juncus gerardi	1692.8	5	79	371.0	4	91	841.2	4	91
Limonium vulgare	857.0	2	83	643.4	4	76	636.5	2	81
Plantago maritima	235.9	4	63	379.5	4	85	900.5	3	90
Puccinellia maritima	1805.7	5	81	1002.6	4	91	177.0	2	56
Triglochin maritima	700.4	1	80	997.1	5	81	473.1	3	87