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Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient

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Summary

1 The relationships between soil development, vertical vegetation zonation, vegetation succession and herbivory by Brent geese, *Branta bernicla*, were studied in a coastal salt marsh. We were able to analyse up to 100 years of salt marsh development by comparing sites where vegetation succession had progressed for various periods of time. These data were related to a continuous daily record of high water levels measured since 1824.

2 Most elevational variation in edaphic conditions (and therefore vertical vegetation zonation) could be attributed to variation in height of the sandy subsoil, as rapid dune formation occurs on the beaches early in succession. In the intermediate part of this elevational gradient, the maximum annual increase of 1.2 mm of silt corresponded to an annual increase of 5.6 g N m^{-2} in the topsoil (0–50 cm). The average sea level rise in this area over the last 170 years was 0.63 mm year^{-1}. A sedimentation model suggests that this has had strong effects on sedimentation and the annual inundation frequency in the mid-part of the elevational gradient, thus affecting vegetation zonation on the salt marsh. For the major part of the investigated transects, sea level rise has probably speeded up succession due to an increased rate of sedimentation.

3 The occurrence and dominance of all plant species were recorded in 3927 plots, and and for the 11 most common species response surfaces were calculated for their dependence on elevation and transect age. Most plant species were clearly separated along these axes. Most halophytic species, which were preferred by the geese, occurred early in succession and low on the gradient, where we observed the highest densities of Brent geese grazing. Forage quality of *Festuca rubra* increased towards the lower salt marsh. Other preferred forage species (*Puccinellia maritima* and *Plantago maritima*) were gradually displaced during succession by the tall grass *Elymus athericus*, especially in the mid- and upper salt marsh. Few geese grazed in areas where *Elymus* was dominant.

4 Herbivores first increased in numbers but then declined along a gradient of primary productivity. We propose that declining forage quality (due to changing vegetation composition during succession) is a better explanation for this pattern than the classic explanation of predator control of herbivores at high levels of primary productivity. This quality threshold hypothesis, as an alternative explanation of the exploitation ecosystem hypothesis, is expected to hold especially where smaller (quality-sensitive) herbivores such as geese are present.

5 Grazing by cattle in a 200-year-old part of the salt marsh led to the disappearance

of *Elymus athericus*, to establishment of early successional halophytes and a return of Brent geese. Grazing by a larger herbivore therefore facilitated conditions for smaller herbivores by preventing the dominance of plant species that were good light competitors, and thus improved forage quality. Populations of these small herbivores could then become regulated by predators, although none was present at our site.

Introduction

Vegetation succession on initially bare substrates involves the accumulation of nutrients in the soil, leading to an increase in nutrient availability, an increase in plant biomass and changes in species composition of the vegetation (Crocker & Major 1955; Bormann & Sidle 1990; Olff *et al*. 1993). Herbivore densities are predicted to increase with increasing primary production (Oksanen *et al*. 1981; McNaughton *et al*. 1989), until a level of primary production is reached where either regulation of herbivores by predators becomes important (Hairston *et al*. 1960; Oksanen *et al*. 1981) or where the food quality of the plant biomass itself becomes a limiting factor to herbivores (van de Koppel *et al*. 1996). This latter effect may occur when tall, late successional plant species (with support structures) represent poor quality forage. A simultaneous analysis of changes in soil nutrients, plant species' abundances and herbivore densities during primary succession has not yet been performed for any terrestrial ecosystem, and may provide a test of these contrasting explanations.

The salt marsh in the eastern part of the island of Schiermonnikoog offers an opportunity for investigating the interactions between soil changes, vegetation and herbivory, since different stages of salt marsh development are spatially contiguous, as the island is gradually extending eastwards. The formation of primary dunes on the islands leads to differences in elevation that are associated with differences in inundation frequency and sedimentation rate and result in the vertical zonation of salt-marsh vegetation (Gray 1992; De Leeuw *et al*. 1993). Besides changing nutrient availability, shifts in tidal inundation rates may explain part of the observed successional dynamics. The potential importance of this was investigated by modelling the changes in the tidal inundation frequency during the last 100 years using data on sea level change and silt accretion.

The area is important for spring staging of Brent geese, *Branta bernicla* (Prop & Deerenberg 1991). During April and May, the geese increase their body mass by about 33% while foraging in this area (Ebbinge 1992) and variation in their breeding success in the Arctic could be partially explained by their

body weight at the end of spring staging (Ebbinge 1992). This means that selection of a suitable area for foraging, based on the presence of appropriate food plant species, is important for the geese. The large increase in body size is only possible through very selective foraging for only those plant species of high nutritional quality (Prop & Deerenberg 1991). Since the geese leave the area in late May (at the start of the growing season) they might not be able to exert much control over the vegetation composition of this salt marsh, in contrast to the situation on their breeding grounds (Kerbes *et al*. 1990; Hik *et al*. 1992; Srivastava & Jefferies 1996).

We examined the long-term dynamics of inundation frequency, silt accretion, plant species distribution and Brent goose densities at different elevations on the salt marsh, utilizing the salt-marsh chronosequence. We hypothesized that silt accretion and soil nitrogen accumulation during primary succession are linked with an increase in goose densities, up to a point where unpalatable plant species become dominant in the vegetation, which becomes unattractive for the geese. Bigger herbivores with a lower requirement for high-quality forage, however, may be able to utilize such late successional species and, may again attract geese by removing tall, productive, relatively unpalatable species (facilitation). This hypothesis was tested in a late successional stage on the salt marsh at Schiermonnikoog, where we analysed the effect of cattle grazing on vegetation composition and goose densities.

Outline of the system and hypotheses

Figure 1 gives a schematic view of the process of salt-marsh formation on Schiermonnikoog, one of the Dutch West Frisian islands 53°30′N, 6°10′E). In the first stage, embryonic dunes are formed on bare beach surfaces, mainly due to sand trapping by *Elymus farctus*. During the next phase of dune succession, establishment of *Ammophila arenaria* and continued sand trapping leads to formation of large dunes. After dunes are formed, the sand flat behind the dunes is no longer frequently inundated by tidal water from the North Sea: inundation occurs only from the Wadden sea at high spring tides, and the reduced
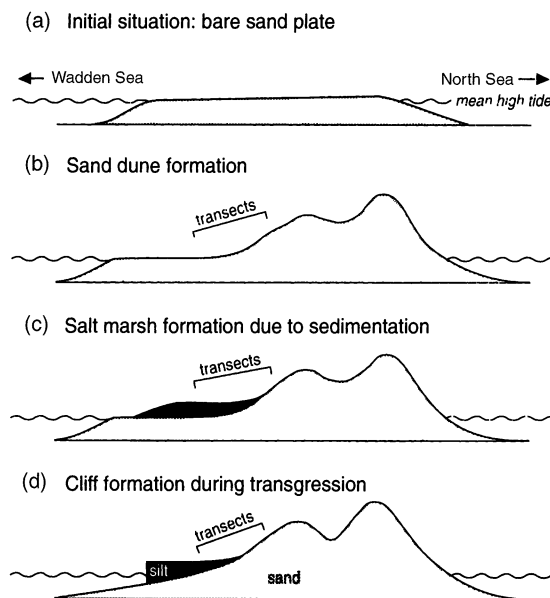
(a) Initial situation: bare sand plate

(b) Sand dune formation

(c) Salt marsh formation due to sedimentation

(d) Cliff formation during transgression

Fig. 1 Four stages of salt-marsh formation on coastal bar islands; the black layer represents the silt that is deposited on the sandy subsoil.

turbulence of the water results in silt sedimentation. Inundation rates decrease to zero towards the foot of a dune, leading to decreased sedimentation, whereas at the lowest elevational positions, high rates of water movement also prevent sedimentation. Sedimentation will therefore be highest at intermediate elevational positions on the young salt marsh (Fig. 1c). During episodes of strong sea level rise, the lower part of the salt marsh may be eroded (Dijkema *et al.* 1991) (Fig. 1d).

A hypothetical scheme for salt marsh development is given in Fig. 2. Increasing sedimentation is expected to lead to a higher nutrient (especially N) availability, resulting in more plant biomass to contribute to silt trapping. In the longer term, the surface level will increase with continued sedimentation, leading to a decreased inundation frequency. Sedimentation therefore results in a negative feedback that increasingly restricts further sedimentation (Fig. 2). The increased primary productivity provides more food for herbivores, which potentially could enhance their density. The forage quality at lower elevations and in the earlier stages of salt marsh succession is predicted to be very high, due to constraints on primary productivity imposed by salinity and waterlogging (i.e. high protein/biomass ratio) (White 1993). However, when herbivores are not able to graze down vegetation to a short sward, tall plants (good light competitors) may become dominant as succession progresses, leading to a decrease in forage quality and to a decrease in abundance of quality-sensitive herbivores.

Description of the chronosequence

Several different stages of salt-marsh development can be found adjacent to one another on the island of

Schiermonnikoog, since changing sea currents cause the island to extend eastwards, so that the western part of the island is the oldest part and young stages of salt marsh development can be found in the eastern part of the island. This process was quantified by mapping the vegetated areas from aerial photographs, taken in 1927, 1952, 1969 and 1980 (Fig. 3). In addition, we used a topographical map (1:50 000) surveyed in 1853 that gave a good indication of the extent of vegetated areas. Based on this information, we placed seven transects, representing sites of different stages of salt-marsh development (Fig. 3). Primary succession on these transects was estimated to have progressed by 1992 for 10 years (transect 1), 25 years (transect 2), 35 years (transect 3), 60 years (transect 4) and 100 years (transect 5). We also established two transects on the oldest part of the salt marsh (transects 6 and 7), where silt accretion has occurred for at least 200 years and grazing by heifers from local farms has taken place for most of that time (Bakker 1989). In 1972, grazers were excluded from transect 6 in order to study the effect of grazing on the vegetation composition (Bakker 1989). Each transect was positioned at the foot of a dune slope (Fig. 1). Along the length of these transects we determined elevation, rates of silt accretion and nitrogen accumulation, vegetation composition and faecal dropping rates of Brent geese (reflecting duration of grazing measured over the whole season). Transects 6 and 7 were not used in the reconstruction of salt-marsh succession, since we expected that cattle grazing had had a strong impact on the species composition of the vegetation.

During the early 1980s, the prime area for grazing by Brent geese was in the vicinity of transect 3. Since then, the prime area for grazing has moved gradually eastwards, and was located in the vicinity of transect 2 in the early 1990s (R. Drent, personal communication).

Methods

ELEVATION MEASUREMENTS AND SOIL SAMPLING

Each transect consisted of a grid of 11 columns and a variable number of rows of 1-m² plots (51–60, depending on the local topography) located adjacent to each other in a grid, with the longest dimension of the grid extending up the slope of the main elevational gradient. For every 1-m² plot we measured elevation (m) with respect to Dutch Ordnance Level (NAP) using a theodolite. In the middle of each plot we took a soil sample with an auger, resulting in a total of 561–660 soil samples for each transect. In each sample, a clear distinction could be made between the subsoil consisting of coarse sand, and a dark, organic, silty sediment layer situated on top of this. The thickness of the silt layer was measured for every sample. Elevational variation has two components, the time-inde-
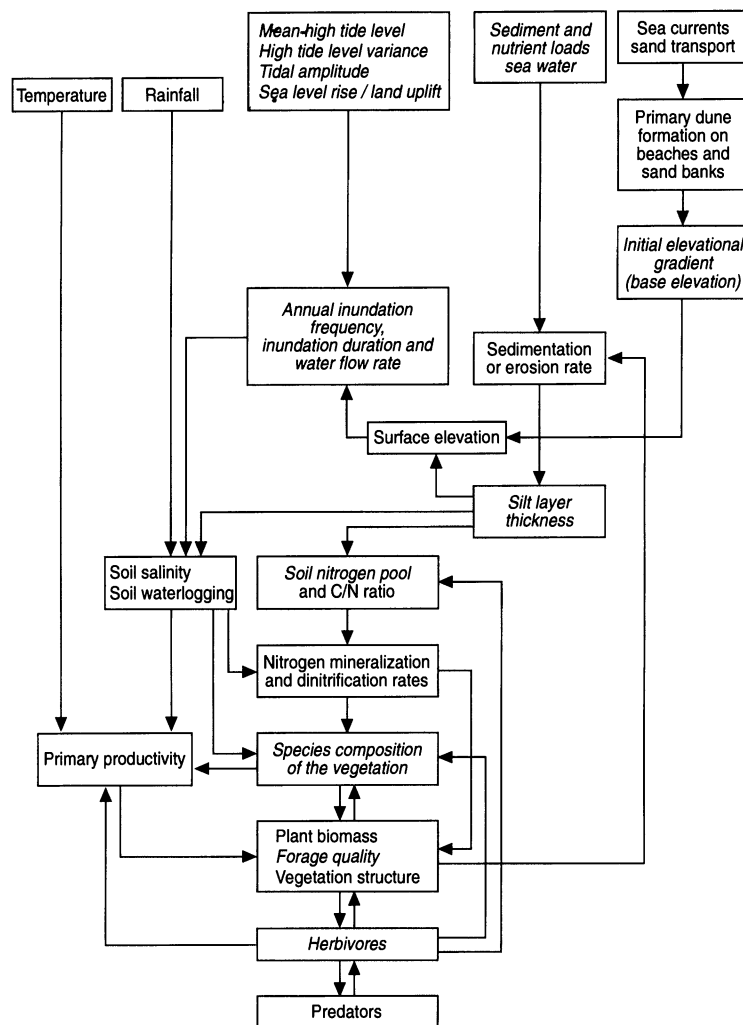
Fig. 2 Schematic view of the relationships between climate, sea level, geomorphology, soil development, vegetation succession, herbivores and predators in coastal salt marsh ecosystems. The features given in italics were investigated in the present study.

pendent elevation of the sandy subsoil (base elevation) and the time-dependent thickness of the silt layer. Surface elevation is thus correlated with age, but by using base elevation (surface elevation minus silt layer thickness), succession can be reconstructed for a given location, and the dependence of silt accumulation and plant species composition on this independent variable can be studied.

At three positions along each transect (low, middle and high elevations) we measured the amount of nitrogen in the topsoil (0–50 cm) by taking samples from the soil layers at 0–5 cm, 5–25 cm and 25–50 cm. Whenever the border between sand and silt fell within one of these layers, we treated that layer as two separate samples. Ten random samples were taken per transect and position and separated into layers, and equivalent samples were pooled prior to the chemical analysis. The bulk density of each layer was determined using volumetric rings (100 cc). The samples were dried for 48 h at 70 °C and finely ground. Total nitrogen concentrations were determined using a Carlo-Erba element analyser. The N accumulation per layer was then calculated by multiplying the N

concentration by the bulk density and the thickness of each layer, and these values were added for all layers between 0 and 50 cm to obtain the total N amount in the top soil. This N amount was then related to the thickness of the silt layer using linear regression analysis.

SEA LEVEL RISE, INUNDATION FREQUENCY AND SEDIMENTATION MODELLING

High-water levels of each tide have been recorded by Rijkswaterstaat at Schiermonnikoog since 1965. For investigations of longer-term changes we also used similar data recorded at the mainland stations of Zoutkamp (1824–36), Oostmahorn 1927–69 and Lauwersoog 1970–93. Due to the construction of local embankments along the mainland coast, we could not use the same station for the whole period, but at the time periods selected the sites were relatively unaffected by these local embankments and therefore could be used as an indication of high water levels at Schiermonnikoog (K. Doekes, Rijkswaterstaat, personal communication). All data were converted to give an
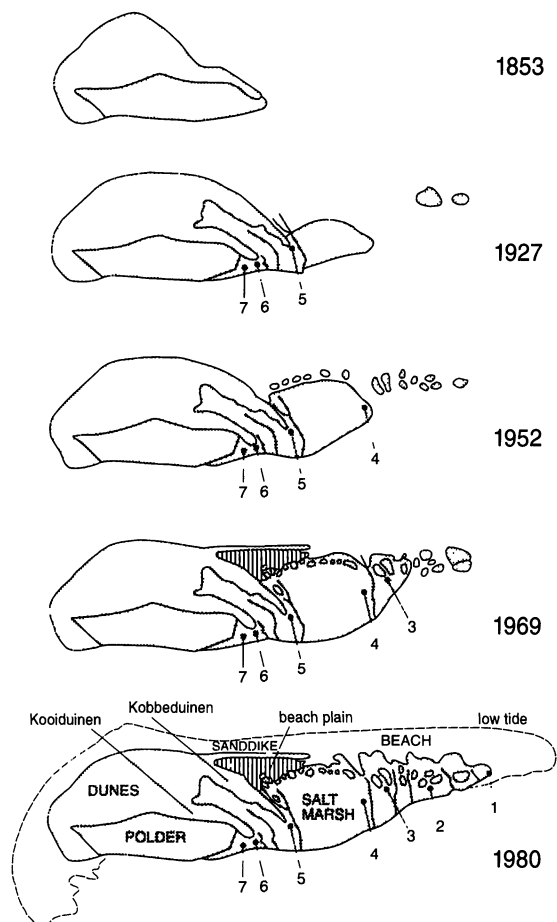
Fig. 3 Reconstruction of salt-marsh development on the Dutch island of Schiermonnikoog. Vegetated areas were mapped from aerial photographs 1927–80 and a topographic map (1853, 1:50 000). Three major vegetation types were distinguished: salt-marsh vegetation (heavily shaded), dry-dune vegetation (lightly shaded) and dune-slack vegetation (hatched). The numbers refer to the position of the different aged transects where salt marsh succession in 1992 had progressed for about 10 years (1), 25 years (2), 35 years (3), 60 years (4), 100 years (5) and 200 years (6, 7).

annual mean tidal height. We obtained the average tidal transgression frequencies at Schiermonnikoog (number of times a location at a given elevation is inundated each year) for 5-cm height classes, over the period 1965–92. From these data we calculated the parameters of a regression equation that predicts the annual inundation frequency of a site based on its surface elevation and the annual mean height of tides.

We then utilized the data on silt accretion along the transects of different ages to calibrate a sedimentation model (outlined in Appendix 1), which enables the silt layer thickness at any time at any base elevation to be predicted. The model was developed to investigate whether the observed sedimentation patterns could be understood from a few simple geomorphological and hydrological principles. It was used to evaluate the consequences of the observed sea level rise on sedimentation in this salt marsh.

PLANT SPECIES DISTRIBUTION

During June and July of 1991, we determined in each plot which species were present, and which were the three most abundant species (highest percentage cover, determined subjectively); these were called the dominant species. With the use of these rapid methods we were able to assess all 3927 plots, which would not have been possible with more precise techniques.

For the 11 most frequently recorded species, the observed data on presence and dominance were first related to the base elevation (20-cm classes) and age, by calculating the probability of occurrence of each species for each combination of transect age and height class. For the same species, the statistical significance of the dependence on age and base elevation was tested for transects 1–5 (3180 plots) by calculating a second order response surface including a linear interaction term, after logit transformation of the dependent variable, where the probability P of being present or dominant is given by:

$$P = 1/1 + \exp(c_1 + c_2 E + c_3 A + c_4 E^2 + c_5 A^2 + c_6 EA) \quad (1)$$

where $c_1, \ldots, c_6$ are the parameters of the model, E denotes the base elevation, and A denotes the transect age. Each term was tested for entry in a forward stepwise logistic regression analysis. This model has the advantage that the dependent variable is bound between 0 and 1, and that it fits a bell-shaped response surface, which is an ecologically realistic response (Ter Braak & Looman 1986; Huisman *et al.* 1992). Although skewed response surfaces can theoretically occur, they could not be fitted with this approach; a satisfactory technique for fitting skewed models in more than one dimension is not yet available (Huisman *et al.* 1992). We omitted the vegetation data of transects 6 and 7 from this response analysis, since their history of cattle grazing affected species composition (Bakker 1985; Bakker *et al.* 1985; Bakker 1989). Response surfaces were only calculated for those species which occurred in more than 25% of the plots.

We also calculated for each species a so-called dominance index, which was the ratio of the numbers of plots in which a species was one of the three dominants, divided by the number of plots in which it occurred. A low value of this index indicates species that rarely attain dominance, even when present at high frequencies (subordinates), while a high value indicates species that dominate the vegetation as soon as they establish.

FORAGE QUALITY

Data on forage quality were not collected in this study, but we used unpublished data collected by H. H. T. Prins and R. Ydenberg in the vicinity of transect 3 (Fig. 1) in May 1979. Fifteen samples of *Festuca*

rubra leaves were taken at different positions on the elevational gradient, which at that time had undergone about 20 years of salt-marsh development. Only the top parts of leaves were collected, as these were the portions grazed by geese. The plant samples were analysed colormetrically for total N after Kjeldahl digestion. Total N amounts were transformed to crude protein concentrations by multiplying values by 6.25.

BRENT GEESE HERBIVORY

Changes in densities of grazing Brent geese in this chronosequence were made based on counts of faecal densities along transects 1, 2, 3 and 5, which represent 100 years of succession undisturbed by cattle grazing (Fig. 3). Faeces were also counted along transect 7, in order to investigate the effect of cattle grazing on goose herbivory. Along each transect, we placed two parallel, adjacent lines of 10 circular plots, each of 4 m², and all plots within and between lines were separated by a distance of 6 m. The 20 plots were therefore equally distributed along each of the transects. Since transect 6 was surrounded by a stout fence to prevent cattle grazing, which also excluded geese, we could not investigate directly the effect of excluding cattle on densities of geese. On 6, 14, 21 and 28 May 1992 we counted numbers of fresh faecal droppings in every plot, and droppings were removed after each count. Fresh droppings were no more than 7 days old, and could be distinguished visually from older droppings that were sometimes deposited in plots by high tides or wind. The faecal dropping counts were used to calculate weekly dropping rates for each plot. This method gives a reliable estimate of the rate of utilization of vegetation by geese (Prop & Deerenberg 1991). These authors concluded, based on visual observations of grazing, removal rates of vegetation by geese and plant remains in faeces, that *Puccinellia maritima*, *Plantago maritima* and *Triglochin maritima* were the principal food sources of Brent geese. *Festuca rubra* acts as a replacement for *Puccinellia maritima*, when the production of the latter drops. In areas with the highest intensities of grazing by geese (i.e. in the vicinity of transect 2), all newly produced tissue of *Plantago* and *Puccinellia* was effectively removed during the grazing period in April and May (Prop & Deerenberg 1991).

Results

SILT ACCRETION AND NITROGEN ACCUMULATION

We investigated the thickness of the silt layer in relation to base elevation and sediment age (duration of sedimentation) along transects. Average values for 10-cm classes are shown for transects 1–5 in Fig. 4a, together with the number of observations (Fig. 4d).
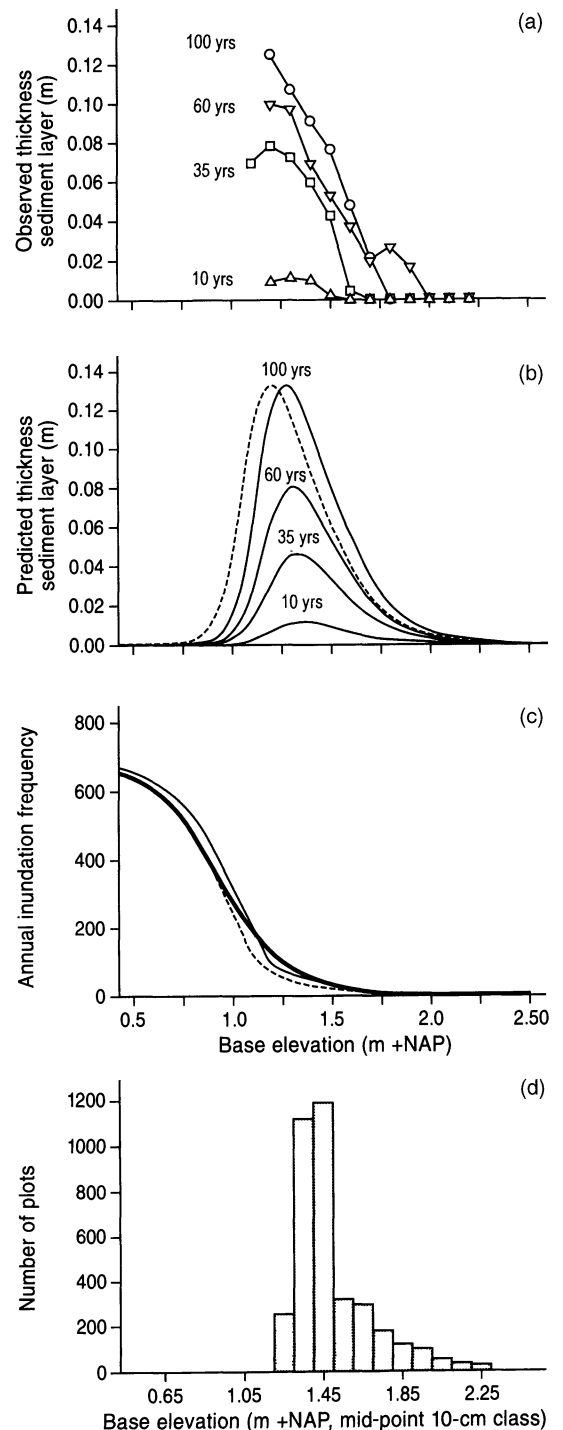

Fig. 4 (a) Dependence of the thickness of the silt layer on the elevation of the sandy subsoil (base elevation) along four transects where vegetation succession had proceeded for 10, 35, 60 and 100 years. Average values are given for 10-cm classes of base elevation. (b) The predicted sedimentation at different base elevations after 10, 35, 60 and 100 years, under the current sea level rise (solid lines) and the predicted sedimentation after 100 years but without sea level rise (dashed line), using the sedimentation model described in Appendix 1. (c) The predicted annual inundation frequency of different base elevations after 0 years of sedimentation (thick solid line), 100 years of sedimentation with the current sea level rise (thin solid line, see Fig. 6) and after 100 years of sedimentation without sea level rise (dashed line). (d) The frequency distribution of base elevation for all investigated transects.

The data show that most plots within transects were situated between 1.30 and 1.50 m above Dutch Ordnance Level (NAP). A thin silt layer was found along the entire gradient on young transects, while a thicker layer occurred at lower elevations on old transects. Within each transect, silt accretion was highest at about 1.3 m above NAP (Fig. 4a). The results indicate that silt accretion over the last century caused a maximum elevational difference of 12 cm, which was rather small compared to differences in base elevation, which were found to exceed 100 cm along the transects (Fig. 4).

Total amounts of nitrogen (g m^{-2}) in the upper 50 cm of the soil significantly increased with the thickness of the silt layer (in cm), according to the regression equation $y = 186 + 43x$, $r = 0.90$, $P < 0.001$ (Fig. 5). The intercept of the regression equation represented an estimate of the initial total nitrogen (186 g m^{-2}) in 50 cm of sand. The slope indicates that the size of the N pool in the topsoil increased by 43 g m^{-2} with every additional centimetre of silt. The maximum accretion of the silt layer was 12 cm over 100 years, equivalent to an increase in total soil nitrogen of 5.16 g m^{-2} year^{-1}.

SEA LEVEL RISE, INUNDATION FREQUENCY AND SILT ACCRETION

Annual mean high water levels have increased in the area at least since 1824, at an average rate of 0.63 mm year^{-1} (Fig. 6; $y = -0.2580 + 0.00063x$, $r^2 = 0.34$, $n = 169$, $P < 0.001$). These tidal data and the observed sedimentation rates (Fig. 4a) were used to calibrate a dynamic simulation model for sedimentation (see Appendix 1). Although the model predictions were not independent from the observations, the simulations (Fig. 4b) were similar to the recorded patterns, and suggested that sedimentation in this salt marsh is a relatively simple geomorphological process, dependent on the relationship between elevation and inundation frequency (tidal height and amplitude) and on water sediment loads. It was not
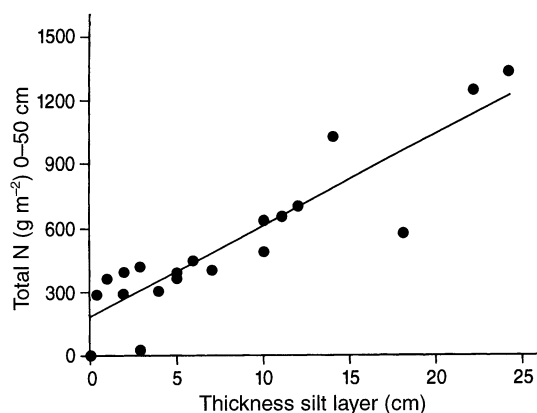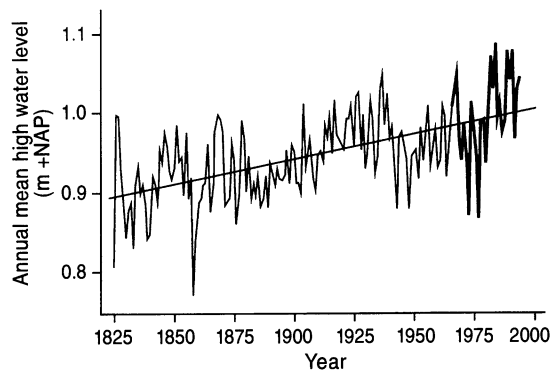

Fig. 6 Sea level rise since 1825 in the eastern part of the Dutch Wadden Sea, reconstructed from different stations (see text), with the linear regression line ($y = -0.2580 + 0.00063x$, $r^2 = 0.34$, $n = 169$, $P < 0.001$). For the recent decades, tidal data from both the mainland station Lauwersoog (thin line) and Schiermonnikoog are shown.

necessary to incorporate a feed-back effect of plant biomass on sedimentation rates in order to produce realistic simulations. The simulations were performed using the observed increase in tidal height (Fig. 6) as input data, and also for a scenario where the sea level had remained at the 1824 level of 0.891 m + NAP (y-intercept of the linear regression in Fig. 6). The simulations showed that the observed sea level rise has had a profound effect on the amount of sedimentation (Fig. 4b) and on the annual inundation frequency (Fig. 4c) for different parts of the elevation gradient. Peak rates of sedimentation have occurred at higher elevations on the marsh, which has resulted in less sedimentation at low elevations and more sedimentation at higher elevations than would have been found without sea level rise. The largest decrease was predicted at 1.10 m above NAP (-5 cm, a reduction of about 50%), with the largest increase at 1.60 m above NAP ($+2$ cm, an increase of about 20%): at 1.20 m above NAP there would have been little change. Without a sea level rise, the inundation would have decreased during succession over the entire gradient from 1.0 to 1.8 m above NAP, but with the observed sea level rise, the inundation frequency decreased during succession at elevations greater than 1.1 m above NAP, and increased at lower elevations (Fig. 4c). The decrease in inundation frequency at higher elevations was less then that predicted in the 'no sea level change' scenario (Fig. 4c). Since most observed base elevations were between 1.35 and 1.55 m above NAP (Fig. 4d), the observed sea level rise has resulted in increases in both sedimentation and inundation in the majority of plots, compared with simulations assuming a constant sea level (the interpolated 1824 level, Fig. 4c)

PLANT SPECIES ZONATION AND VEGETATION SUCCESSION

Only 25 vascular plant species (all halophytes) were recorded in the 3180 plots of transects 1–5, and 11

Fig. 5 Total nitrogen pool in the top 50 cm of the soil in relation to the thickness of the silt layer across different ages (duration of sedimentation) and different base elevations.

species that occurred in more than 25% of the plots were used in the regression analyses (basic data in Fig. 7). A significant logistic regression was fitted, for both presence and dominance of each of these species (Table 1). The effect of age was always significant, indicating that for every species these variables showed a trend with time. Values for presence and dominance for about half of the species reached a maximum during succession (significant quadratic effect of age; Table 1), while corresponding values for all other species either increased or decreased continuously. A similar pattern was found for the effect of elevation. The interaction effect of age × elevation was significant for almost every species (Table 1), which can be interpreted as either the distribution of species along the elevational gradient changed with succession, or the successional dynamics of individual species were different for each elevational position. The interaction term was not significant for the presence/absence data of *Elymus athericus*. The curves based on the calculated logistic regression equations (Figs 8 and 9 and Table 1) gave a good fit to the

recorded observations (compare with Fig. 7). Results of the presence and dominance of plant species were qualitatively similar but the distributions in time and space of dominance were more constrained than those for presence (Figs 7, 8 and 9).

After 10 years of succession on the lowest sections of the transects (base elevation 1.2 m above NAP), the vegetation was dominated by *Spergularia maritima*, *Suaeda maritima*, *Limonium vulgare* and *Puccinellia maritima* (Figs 7 and 8). *Limonium* increased further and maintained dominance along the entire successional sequence on the low salt marsh, while the remainder of the above species decreased in dominance. *Spergularia* disappeared, but *Puccinellia* and *Suaeda* remained present at relatively high frequencies. *Festuca rubra*, *Glaux maritima* and *Artemisia maritima* all increased in presence and dominance during the successional sequence. *Juncus gerardi* increased after 40 years, and became one of the most dominant species in the later stages of succession. The only species which showed a clear maximum in presence and dominance in time was *Atriplex por-*

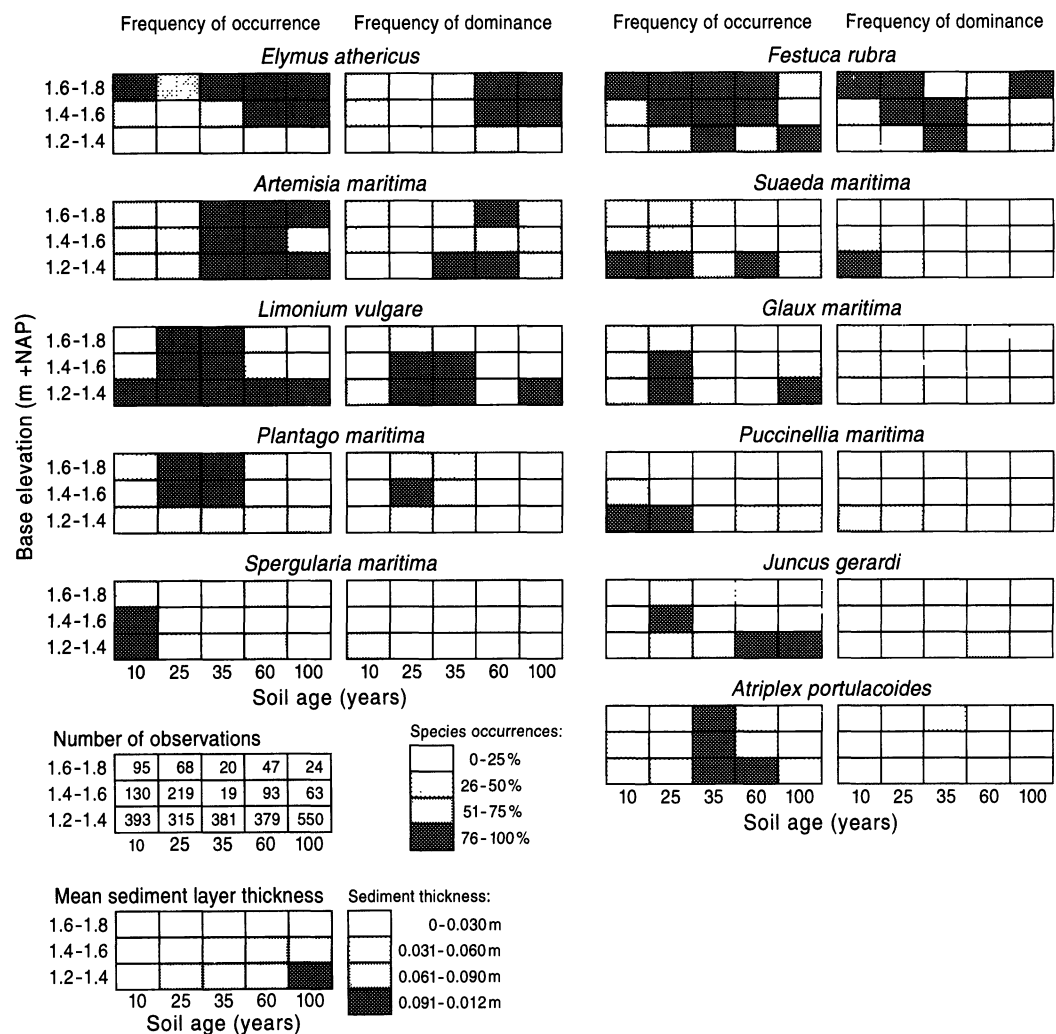**Fig. 7** Observed frequency of occurrence and frequency of dominance (based on cover) of 11 salt-marsh species, as related to transect age (duration of succession) and elevation of the sandy subsoil (base elevation). The average silt layer thickness and the number of observations are given for each combination of age and base elevation class. The darker shades of grey represent higher values of frequency of occurrence or dominance.

Table 1 Parameters of the step-wise logistic regression equation* for the dependence of species presence and dominance on base elevation (in m above NAP) and soil age (in years). The number of years succession had progressed was divided by 100 for the parameter calculation. Also the total abundance (% of plots present or dominant) is given for each species, as well as the dominance index

Species† (with abbreviation)	Regression parameter						Abundance (%)	Dominance index‡
	Age	Elevation	Age²	Elevation²	Age × elevation	Constant		
Presence								
Elymus athericus (*Ea*)	20.52	65.08	−14.96	−16.47	0.00	−64.56	30	0.80
Artemisia maritima (*Am*)	23.37	4.08	−8.30	0.00	−7.93	−7.83	68	0.63
Festuca rubra (*Fr*)	3.70	48.67	−11.83	−12.69	−13.19	−43.30	65	0.72
Plantago maritima (*Pm*)	9.51	22.57	1.52	5.96	5.95	−19.80	50	0.36
Puccinellia maritima (*Pa*)	44.42	92.76	0.00	−34.14	−36.19	−61.38	41	0.39
Juncus gerardi (*Jg*)	101.84	123.48	−14.64	−37.03	−59.18	−103.91	51	0.24
Spergularia maritima (*Sm*)	−7.26	11.59	0.00	−5.17	2.70	−5.16	35	0.29
Limonium vulgare (*Lv*)	15.63	−5.39	−5.85	0.00	−7.44	8.70	80	0.71
Suaeda maritima (*Sa*)	12.35	−5.01	0.00	0.00	−11.44	8.75	58	0.33
Glaux maritima (*Gm*)	45.97	40.81	0.00	−11.95	−34.20	−32.80	56	0.34
Atriplex portulacoides (*Ap*)	22.44	0.00	−11.85	0.00	−6.95	−2.33	48	0.19
Dominance								
Elymus athericus (*Ea*)	9.67	57.08	−12.41	−15.00	5.87	−56.32	24	
Artemisia maritima (*Am*)	22.70	13.45	−10.91	−3.40	−5.90	−15.68	43	
Festuca rubra (*Fr*)	15.65	44.60	−2.32	−12.01	−8.31	−39.70	47	
Plantago maritima (*Pm*)	13.28	34.95	−3.01	−9.72	−7.38	−31.62	18	
Puccinellia maritima (*Pa*)	38.51	134.71	0.00	−50.44	−34.05	−89.17	16	
Juncus gerardi (*Jg*)	158.50	213.28	−26.93	−64.37	−93.87	−179.96	12	
Spergularia maritima (*Sa*)	−109.18	39.22	0.00	−20.55	64.03	−12.65	10	
Limonium vulgare (*Lv*)	43.75	0.00	0.00	0.00	−32.32	0.38	57	
Suaeda maritima (*Sm*)	36.73	120.50	0.00	−43.56	−31.67	−82.40	19	
Glaux maritima (*Gm*)	61.88	41.42	0.00	−12.01	−47.49	−34.78	19	
Atriplex portulacoides (*Ap*)	11.97	−6.47	−19.41	0.00	6.56	2.41	9	

*Parameters indicated by zero did not improve the regression model significantly when added.

†Other species present in less then 25% of the plots not included in the regression analysis (with frequency of occurrence): *Armeria maritim* 15, *Elymus farctus* 6, *Spartina anglica* 7, *Atriplex prostrata* 2, *Cochlearia danica* 2, *Plantago coronopus* 3, *Agrostis stolonifera* 3, *Juncus maritimus* 4, *Ammophila arenaria* 1, *Triglochin maritima* 22, *Aster tripolium* 23, *Carex extensa* 3, *Parapholis stricta* 1, *Sonchus arvensis* 1

‡Calculated as (% of plots dominant)/(% of plots present).

tulacoides. The highest abundances of this species were recorded at sites that had undergone between 40 and 60 years of succession. *Elymus athericus* was never an abundant species on the lowest sections of the transects. *Plantago maritima* occurred in one-third of the plots, but was almost never a dominant species, and did not show a clear successional trend in abundance.

The successional sequence in the middle part of the transects (base elevation 1.5 m above NAP) was different from that described above. *Festuca* and *Limonium* were initially the most dominant species (Fig. 7), but whereas *Festuca* remained abundant, *Limonium* decreased as succession progressed. Both *Elymus* and *Artemisia* increased during succession at these middle elevations and *Elymus* finally became codominant with *Festuca*, while *Artemisia* decreased in the later stages of succession. *Suaeda*, *Glaux*, *Spergularia* and *Puccinellia* also decreased as succession progressed.

At the highest elevations of transects (base elevation 1.8 m above NAP), the successional dynamics in species composition was different again. Initially, *Festuca* was abundant, with some *Elymus* and *Plantago*, but *Elymus* rapidly increased and ultimately became the single dominant in many plots. *Artemisia* decreased after an initial increase.

A different perspective of the regression relationships for *Elymus*, *Festuca*, *Plantago* and *Puccinellia* is provided in Fig. 9. The same regression equations in Table 1 were used, but now the complete distributions along the elevational gradient have been graphed, for the different phases of succession. They show that *Elymus* initially occurred only in the higher part of the salt marsh, but the species has extended gradually to the lower parts of the salt marsh during succession. There was no significant age × elevation interaction, so the maximum values with respect to elevation did not change. Initially, *Festuca* was absent at the lowest levels, it increased in presence and dominance at this elevational position, but at the highest sections of the transects it decreased in dominance, although it remained present. In the upper part of the salt marsh, *Plantago* was present for up to 25 years after the start of succession, but by 100 years it had decreased. In the lower salt marsh, *Plantago* did not change in abundance. At the lower sections of the gradient where it was initially among the most abundant species, *Puccinellia* decreased in dominance during the course of succession, but remained present in many plots.
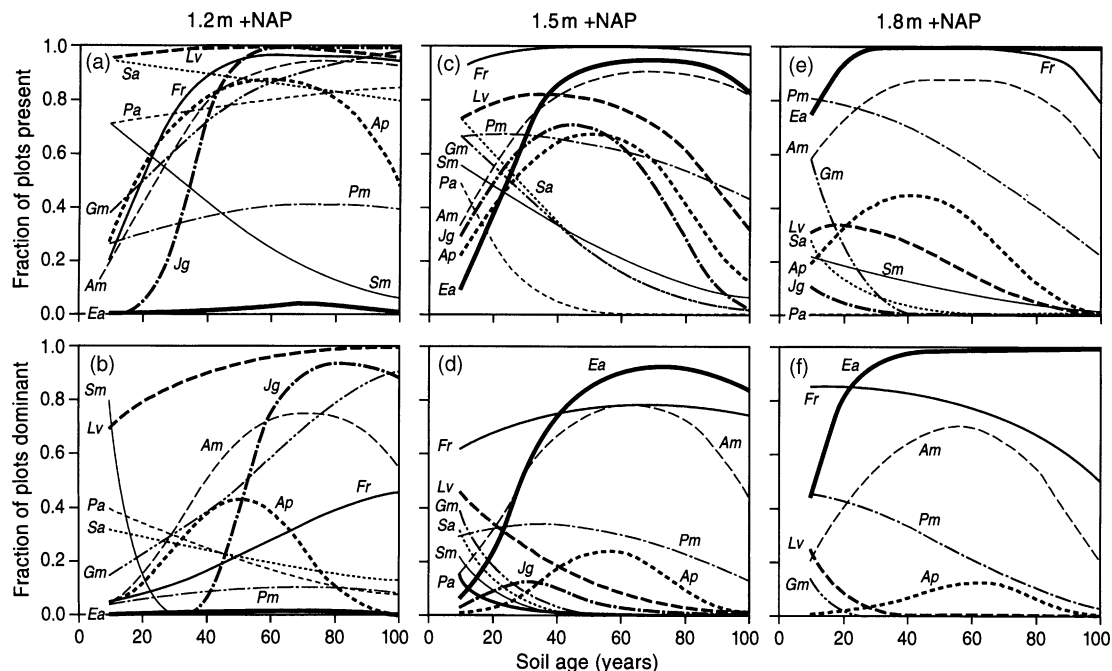
Fig. 8 Calculated trends fitted by logistic regression for 11 salt-marsh species, representing the probability of presence (a, c, e) and dominance (b, d, f) as related to the age of the transect (duration of vegetation succession) at three elevations of the sandy subsoil (base elevation, in m above Dutch Ordnance Level (NAP)). Regression parameters are given in **Table 1.** Although the equations were fitted with both age and elevation as independent variables, a cross-section of the response surfaces at each base elevation is presented here. See Table 1 for complete species names.

FORAGE QUALITY

Data on the composition of *Festuca* leaf tissue (Fig. 10) collected at a 20-year-old successional stage showed that amounts of crude protein in tissues increased from 18 to 24% from the upper to the lower elevations of the salt marsh ($y = -0.0051x + 21.631$, $r = -0.97$, $P < 0.001$).

ZONATION, SUCCESSION AND GEESE HERBIVORY

The highest densities of faecal droppings were recorded at the lower end of the elevational gradient, on the second transect (25 years of age) (Fig. 11). Along younger and older transects, dropping densities were lower. A one-way analysis of variance of the faecal dropping densities within the base elevation range 1.2–1.4 m above NAP yielded a significant difference between transects ($F_{3,44} = 31.95$, $P < 0.001$). A posteriori contrasts showed that the faecal dropping rate along the 25-year-old transect was significantly higher than those along the first and last transects (Fig. 11c; $P < 0.05$). The 35-year-old transect was significantly lower than the previous stage but higher than the last stage ($P < 0.05$), while it was not different from the 10-year-old stage (Fig. 11c). The faecal densities in the first and the last stage of succession (10 and 100 years, respectively) were low, and not significantly different from each other ($P > 0.05$). Clearly, geese preferred within the lower salt marsh the mid-successional stage (25–35 years.).

EFFECT OF CATTLE GRAZING IN A LATE-SUCCESSIONAL STAGE ON VEGETATION ZONATION AND GOOSE HERBIVORY

Transect 7 has undergone 200 years of succession, during which time there has been almost continuous cattle grazing. Transect 6 has also undergone 200 years of succession, but large herbivores have been excluded from this transect in the last 20 years. The differences in vegetational composition between transects 6 and 7 therefore have developed during the last 20 years. This has resulted in the dominance of *Elymus athericus* over the entire gradient in transect 6; in contrast, *Plantago maritima* and *Festuca rubra* have become restricted to the higher part of the transect, while *Puccinellia* has become rare along the whole transect (Fig. 12c; note that low plots (< 1.30 m above NAP) are lacking in these transects). Although the fence along transect 6 prohibited goose grazing, the results from the 100-year-old transect 4 suggest that dominance of *Elymus* (Figs 9b and 11c) would have prevented their grazing even if the geese had had access to the vegetation. In contrast, continued cattle grazing (transect 7) maintained the dominance of early successional salt-marsh species, even after 200 years (such as *Puccinellia*; compare Figs 9h and 12a). Cattle grazing led to strong suppression of *Elymus* (Fig. 12a,c) and allowed the Brent geese to forage on the early successional species that established (Fig. 12b). Faecal densities were higher towards the lower part of the gradient along transect 7 ($y = 36380e - 8.26x$, $n = 20$, $r = 0.86$, $P < 0.001$,
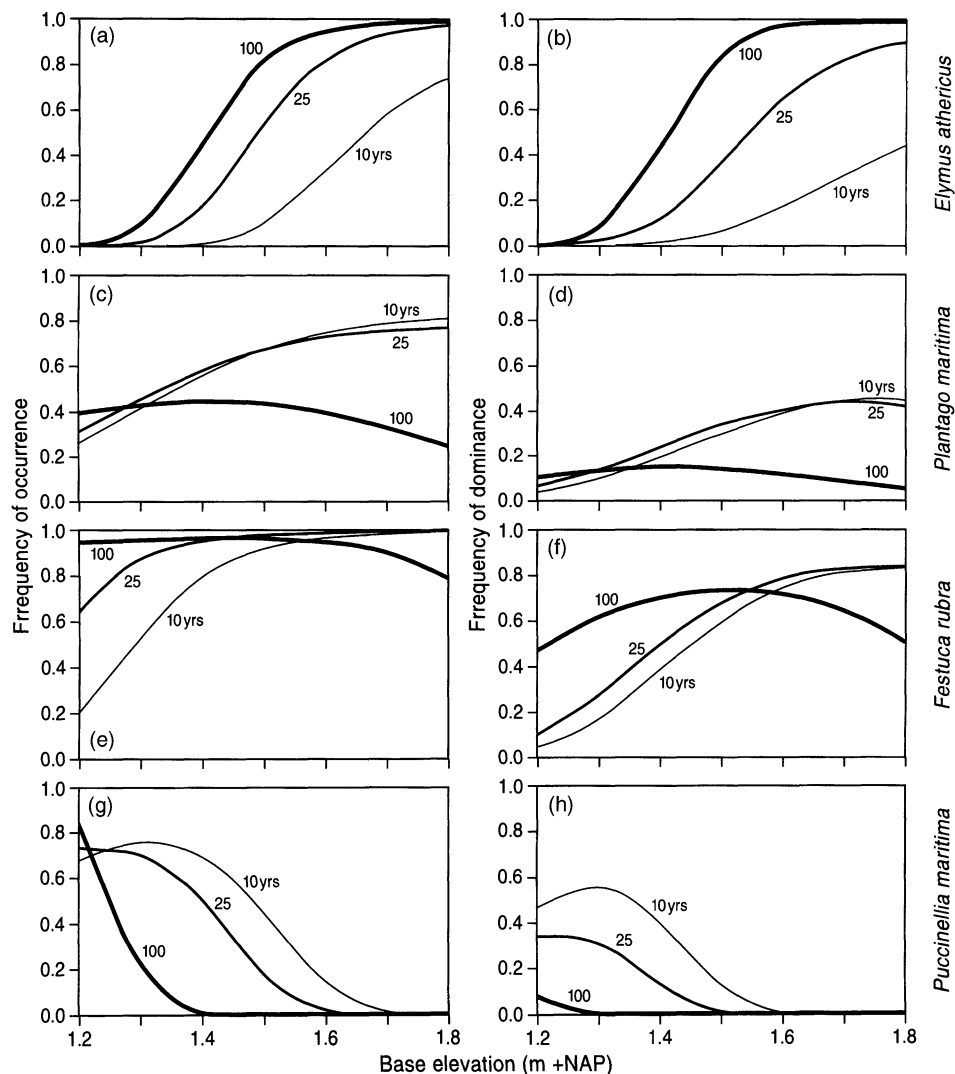
Fig. 9 Changes during succession in vertical distribution along an elevational gradient of four salt-marsh species important as a food source for Brent geese (see text). Base elevation denotes elevation of the sandy subsoil. The same response surfaces are used as in Fig. 8 (see **Table 1** for parameters), but now a cross-section along the elevational gradient is shown at 10, 25 and 100 years of vegetation succession. Plant species abundances are expressed either as the proportion of plots in which the species occurred (a, c, e, g), or as the proportion of plots in which the species was one of the three dominants (b, d, f, h).
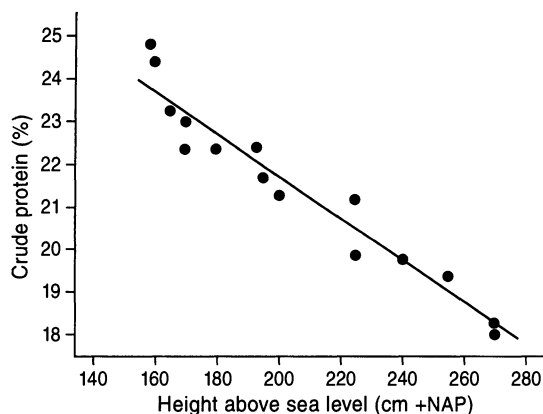

Fig. 10 Tissue crude protein concentrations (6.25 × total N%) of *Festuca rubra* along a elevational gradient in a 20-year-old part of the salt marsh. Only young leaf tips were collected for the analyses, as they are grazed by Brent geese. Note that in contrast to the other figures, the actual surface elevation is given in this graph, not base elevation.

Fig. 12b), where the frequently dominant *Triglochin maritima* is especially favoured by geese (Fig. 12; personal observations; see also Mulder *et al.* 1996).

Discussion

Changes in salt-marsh ecosystems result from a complex interplay of changes in geomorphology, flooding regime, water sediment loads and salinity, soil characteristics, vegetation type and herbivory, and this may produce many feedbacks (Fig. 2). Geographic variation in the relative importance of these factors in their effect on sedimentation and surface elevation will lead to different geomorphological types of salt marshes (Dijkema 1987; Adam 1990; Gray 1992; de Leeuw *et al.* 1993). Primary productivity and species composition of the vegetation depend on the inundation frequency, which in turn depends on geomorphology. However, the vegetation also alters the
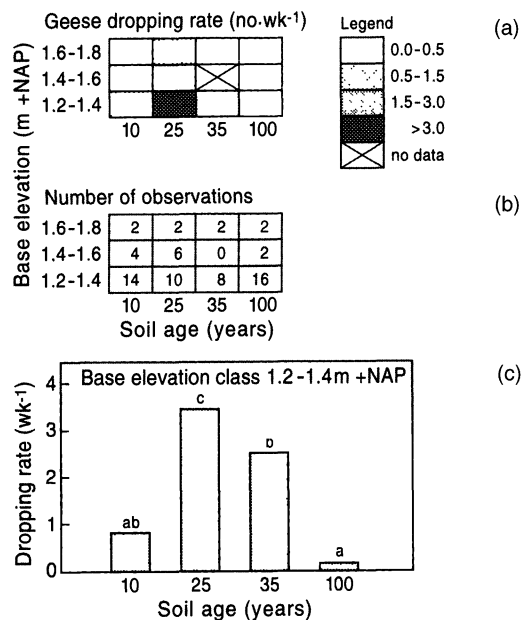
Fig. 11 (a) Average faecal dropping rates (number m^{-2} weeks^{-1}) of geese at different elevations of the sandy subsoil (base elevation, in m above NAP) (Dutch Ordnance Level) (as 20-cm height classes) and successional stage. (b) The number of observations for each combination. (c) Mean faecal dropping rates at the lowest base elevation class. Means with the same letter were not significantly different (Student–Newman–Keuls test after one-way analysis of variance).
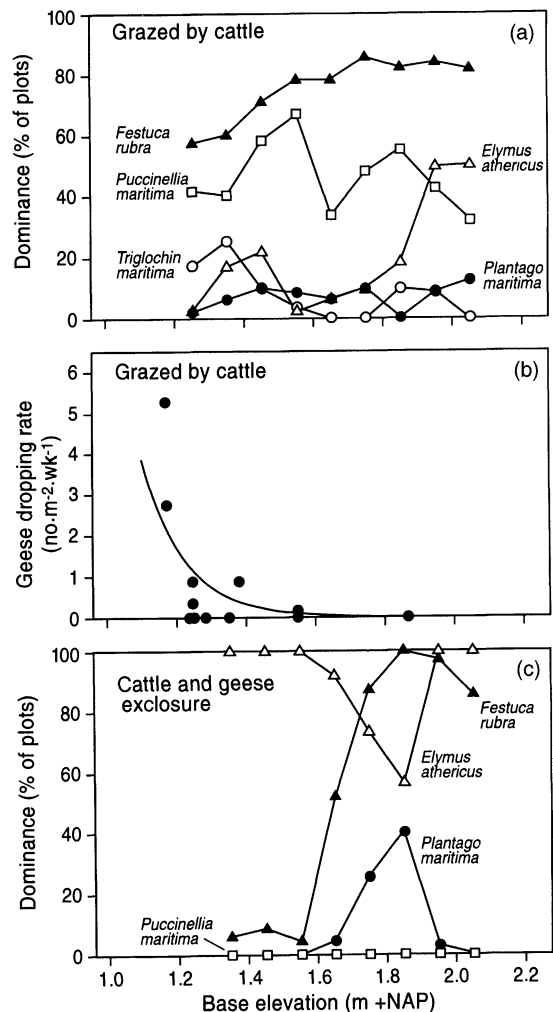

Fig. 12 The distribution of (a) various plant species important for geese grazing along the elevational gradient of transect 7 (200 years of succession, grazed by cattle for the last 20 years) and (b) faecal deposition rates of Brent geese, *Branta bernicla*, along this transect ($y = 36380e^{-8\,26x}$, $n = 20, r = 0.86, P < 0.001$), and (c) the distribution of plant species along transect 6 (200 years of succession, ungrazed by cattle and geese for the last 20 years).

geomorphology by trapping sediment, thereby altering the inundation frequency and inducing soil changes. Herbivores respond to the vegetation because of their preference for certain plant species, directed by their physiological and morphological constraints in handling food. Herbivores, however, also affect the salt marsh vegetation, by removing plant biomass and altering the light environment, nutrient availability and soil salinity (Bakker *et al.* 1985; Srivastava & Jefferies 1996; Wilson & Jefferies 1996).

In our study site, most elevational variation could be linked to elevational differences in the sandy subsoil (Figs 1 and 2). These 'coastal bar' type salt marshes of the Wadden Sea are characterized by low sediment loads in the water, resulting in relatively slow sedimentation rates. In contrast, salt marshes along river deltas of the Dutch, British and German North Sea coasts are generally characterized by less initial elevational variation (little sand dune formation), and much higher rates of sedimentation (> 1 m per century; De Leeuw *et al.* 1993). In these salt marshes, most elevational variation is caused by different periods of sedimentation, so that lower salt marshes are also younger salt marshes. This is not true for the coastal bar-type salt marsh described in this study: each elevational position has its own characteristic successional sequence (Figs 7 and 8). A third geomorphological type of salt marsh is found along the Hudson Bay coast and along the Baltic coast. In these cases, most elevational variation ori-

ginates from isostatic land uplift attended by slow sedimentation rates, and here again lower elevations are of a younger successional age (Jefferies *et al.* 1979).

The relatively strong sea level rise occurring in this part of the Wadden Sea over the last two centuries (Fig. 6) has probably had a strong impact on vegetation zonation and succession on the salt marsh. Interestingly, this appears to have led to a decreased rate of sedimentation on the lowest salt marsh, and increased sedimentation on the higher salt marsh, with little change in the intermediate zone (Fig. 4b). However, the majority of plots were located at relatively high elevations, so increased sedimentation has probably occurred in most plots. Since increased silt accretion leads to increased nitrogen accumulation (Fig. 5), it is likely to be an important cause of plant species replacement and, hence, vegetation succession may have been speeded up by sea level rise.

The simulations showed that the assumption of a

constant sedimentation rate during succession produced predicted patterns of silt accumulation that agreed well with the observations (Fig. 4). This implies that the increase in vegetation height and density during succession does not exert a profound effect on sedimentation rate.

A general dogma of salt marsh zonation is that the lower vertical limit of species is controlled largely by tolerance of tidal factors, while the upper limit is fixed by interspecific competition (Snow & Vince 1984; Gray 1992; Pennings & Callaway 1992). Rozema *et al.* (1985) tested the salt and flooding tolerance of 12 species from this same salt marsh in growth experiments, and concluded that their ranking in salt tolerance corresponded to the order of their vertical zonation on the salt marsh. A similar conclusion was reached by Snow & Vince (1984), who found that the ability of species to tolerate extreme edaphic factors (salinity, flooding) determined the seaward limit of distribution within a salt marsh. When potential distributions overlapped, especially at the higher end of the gradient, they found that competition was important in maintaining the zonation pattern. An interesting result of the present study is that the upper and lower elevational limits of species changed during succession (Fig. 9), possibly as a result of changing competitive abilities associated with nutrient accumulation. Perennial grasses, such as *Elymus athericus* and *Festuca rubra*, are able to extend towards the lower salt marsh (Fig. 9) with the progress of nutrient accumulation. *Elymus* moved about 40 cm down the elevational gradient, while silt accretation was only 12 cm at its maximum, indicating that the increase in surface elevation was not the main explanation for the behaviour of this species in different transects. It is possible that the salt tolerance of some species is increased at higher nutrient availability, or that the soil salinity decreased with biomass accumulation towards later successional stages (see Srivastava & Jefferies 1996). Small halophytes, such as *Plantago maritima* and *Puccinellia maritima*, became much less abundant at higher elevations, but remained at lower elevations as silt accumulated. Competitive interactions possibly may become important at progressively lower elevations as succession continues. However, *Elymus* does not become dominant below 1.3 m above NAP during the first 100 years of succession (Fig. 9b), so that the most salt-tolerant species can survive in a refugium at the lower elevations. Rozema *et al.* (1985) found that *Elymus* was one of the least salt-tolerant species, while *Puccinellia*, *Glaux* and *Salicornia* were the most salt-tolerant species occurring in this marsh.

With increased nitrogen accumulation due to sedimentation, plant species with a low stature (*Puccinellia maritima*, *Salicornia* sp., *Spergularia maritima*) were replaced by taller species (*Elymus athericus*, *Artemisia maritima*, *Atriplex portulacoides*), which suggested that light competition becomes more important with increasing nutrient availability (Tilman 1985; Olff *et al.* 1993). However, interspecific differences in colonization ability may also be important in accounting for the changes. Annual salt marsh plants (*Suaeda*, *Salicornia*, with high seed production) were the first to be present and the first to disappear along transects. This may imply that a trade-off between colonization and competitive ability (Tilman 1994) was important in determining the successional pattern of species. Indirect evidence for this can be obtained from the dominance index data (Table 1). The perennials *Limonium*, *Elymus*, *Festuca* and *Artemisia*, which increased in later successional stages, had high dominance indices, which indicated that whenever they established they rapidly became dominant. Low values for the dominance index were recorded for short-lived plants (like *Salicornia*) which decreased in abundance after 10 years of succession. Although they sometimes occurred in high frequencies, they rarely became dominant. In this marsh, therefore, a low value of the dominance index is indicative of high colonizing ability, while a high value indicates high competitive ability.

High densities of Brent geese were observed on the lower part of the elevational gradient in mid-successional stages (25–35 years) (Fig. 11). We observed a good correspondence between the distribution of goose droppings and high abundances of three of their principal food species, *Festuca* (maximally 24% protein in May), *Puccinellia* (28% protein in May) and *Plantago* (28% protein in May) (Figs 7, 8 and 11; protein concentrations from Prop & Deerenberg 1991). *Elymus*, which dominated the highest part of the gradient, had a much lower protein content (12% protein; Bakker 1989) and was avoided by the geese. The restriction of geese to lower elevations was probably not only determined by the distribution of food species, but also by an increasing quality of plants of the same species at lower elevations (Fig. 10). Other studies are in line with the conclusion that 'stressed' plants are more beneficial to herbivores because their nutritional quality is higher (Breman & De Wit 1983; Bink 1986; White 1993; Crawley 1997). Although *Puccinellia* dominated the lower part of the first transect (10 years of succession; Figs 7 and 8), we observed low dropping densities here, probably because the plants were too small and sparsely distributed. With the increasing dominance of *Festuca* and *Elymus* on the lower and mid-sections of the transects, *Puccinellia maritima* and *Plantago maritima* decreased in dominance, and the abundance of goose droppings declined (Fig. 11).

Classic exploitation theory (Hairston *et al.* 1960; Oksanen *et al.* 1981; Oksanen 1990; Crawley 1997) predicts that productive environments are capable of supporting natural predators that are sufficiently abundant to keep herbivores scarce, but below a threshold level of primary productivity the impact of natural predators becomes trivial because the sec-

ondary productivity of their prey becomes too low to sustain the predator populations. Below this threshold, herbivore densities decrease towards lower primary productivity because they become increasingly limited by their food. This so-called exploitation ecosystem hypothesis to explain why herbivore densities level off at intermediate productivity is, however, an unlikely explanation for the patterns observed in this study, since the geese have no natural enemies on this island. Instead we think that vegetation succession, attended by nutrient accumulation, is generally associated with increasing abundance of superior light competitors (tall species like *Elymus* and *Artemisia*). A high investment in structural tissues is an important trait enabling these species to attain dominance under productive conditions. However, these tissues are generally low in nutrients (especially nitrogen), and difficult to digest, which reduces the quality of tall plants as a food source for herbivores. Furthermore, tall rhizomateous grasses like *Elymus* withdraw nutrients efficiently from senescing leaves (enabling them to regrow fast in the next spring), so that large quantities of standing dead material (of low forage quality) are left in autumn (Bobbink *et al.* 1989). In the subsequent spring, these dead leaves can comprise up to 50% of the above-ground biomass (van de Koppel *et al.* 1996), making it difficult for the geese to select fresh leaves. We call this explaination of why herbivore densities may peak at intermediate productivity the quality threshold hypothesis (van de Koppel *et al.* 1996; Huisman *et al.*, in press; Prins & Olff, in press). An important consequence of quality limitation for herbivores at high net primary productivity is that it may cause multiple stable states in plant–herbivore systems (van de Koppel *et al.* 1996). Although we did not measure population sizes, we hypothesize that productive environments may not be capable of supporting large populations of smaller herbivores because the food quality is too low, and herbivore densities will thus show a maximum at intermediate levels of net primary productivity. In a recent review, Cebrian & Duarte (1994) found that herbivore consumption across ecosystems was especially low in areas with very high plant production. More data on herbivore densities along productivity gradients are needed to show whether the observed patterns are explained best by the exploitation ecosystem hypothesis or the quality threshold hypothesis.

We found that cattle grazing of vegetation in a late successional stage that would otherwise be dominated by *Elymus athericus* caused the re-appearance of early successional species such as *Puccinellia maritima*, and also the re-appearance of Brent geese (Fig. 12). Cattle grazing caused plant species normally characteristic of the lower part of the elevational gradient to colonize these higher positions on the elevational gradient (Fig. 12; see also Bakker *et al.* 1985; Bakker 1989). Cattle can utilize forage of a much lower quality than geese, and sometimes they prefer *Elymus* (Bakker

1989). This prevents *Elymus* from becoming dominant, and leaves are grazed before they can become standing dead biomass. Large herbivores, such as cattle, therefore appear to prevent the mechanisms stated in the quality threshold hypothesis from becoming operative, and may perhaps even induce predator control of small herbivores. Since cattle grazing in these salt marshes causes the sward to be opened without impoverishing the soil (Bakker 1989), and increases salinity in the top soil (Bakker *et al.* 1985), these observations support the hypothesis that light competition, together with increasing nutrient availability (due to sedimentation) and decreasing soil salinity, has caused the disappearance of early successional halophytes. Whereas cattle were able to arrest succession and cause a retrogression (Bakker 1989), the geese were apparently not able to prevent *Elymus* from becoming dominant. Large effects of geese on vegetation composition do, however, occur in Arctic breeding grounds, where they forage during almost the entire period of vegetation growth (Bazely & Jefferies 1989; Ruess *et al.* 1989; Hik *et al.* 1992; Srivastava & Jefferies 1996). On the salt marsh at La Pérouse Bay, Canada, vegetation succession in the presence of goose grazing proceeds from a *Puccinellia–Carex* assemblage to a *Calamagrostis–Festuca* assemblage, changes which have been attributed to isostatic uplift. The geese delay vegetation succession in this area but are also not able to stop it completely (Bazely & Jefferies 1985). In both this case and on our study site, the geese seem to depend on vegetation that is at a particular stage in a succession that is primarily driven by a combination of changes in geomorphology and soil conditions.

Acknowledgements

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Appendix 1

A SIMPLE INUNDATION/SEDIMENTATION MODEL

In order to understand the process of sedimentation in this type of salt marsh and to analyse the consequences of the observed sea level changes for sedimentation, zonation and succession, we developed a sedimentation model for which the parameters can be fitted from simple measurements.

After the initial phase of sand-dune formation, a rather steep elevational gradient exists, which is important in understanding the spatial variation in sedimentation rate. The lower part of the gradient is inundated every day, and the sedimentation rate will be almost zero, mainly because the flow rate of the water is high. At the higher end of the gradient, inundation takes place only very rarely, so sedimentation is low or zero. In the intermediate part of the elevational gradient (initially the elevation of the sandy subsoil) sedimentation is expected to be at its maximum. The dependence of annual transgression frequency (T) on elevation (E) can be described by the empirical model:

$$T = \frac{m}{1 + e^{a(E-H)}} \tag{1}$$

where m is the maximum number of tides per year, a is a parameter denoting the relative rate of decrease in T with E, and H is the annual mean high water level (m above NAP), which might change with time due to sea level rise. Note that H in this cumulative model only represents the mean high tide provided the levels of the high tide follow a symmetric distribution; this assumption is valid in this case. If H shows a simple linear change with time (t) over a certain period then:

$$H = h_0 + rt \tag{2}$$

where h_0 is the mean high water level at the start of the period, and r is the annual rate of change in mean high water level.

As outlined above, the annual sedimentation rate S depends on the transgression frequency, with a maximum at intermediate frequencies. A simple model for this is:

$$S = \frac{bT}{1 + e^{cT}} \tag{3}$$

where the empirical parameters b and c determine the height and width of the curve. When b and T are both positive, the function described by eqnuation 3 goes through the origin, then rises with T towards a maximum, and then declines towards zero.

The elevation of a point in a certain year will be determined by the elevation in the previous year, plus the sedimentation in that year, so that:

$$E_{t+1} = E_t + S \tag{4}$$

Combining equations 1, 2, 3 and 4 results in the final sedimentation model:

$$E_{t+1} = E_t + \frac{bT}{1 + e^{cT}}$$

with

$$T = \frac{m}{1 + e^{(a(E_t - h_0 - rt))}} \tag{5}$$

Dynamic simulation of E using this equation with an annual time step allows for the calculation of the soil surface elevation starting from any initial elevation E_0 (base elevation) after any number of years.

The thickness of the silt layer (D) after n years can then be calculated as:

$$D_n = E_n - E_0 \tag{6}$$

Parameter Estimation

The values of the parameters h_0 and r can be obtained from a linear regression of the observed annual mean high tide vs. time. In our case, these data were measured from 1824 to 1993, and the annual mean high tide indeed significantly increased ($R^2 = 0.34$, $n = 169$, $P < 0.001$).

The parameter value for a can subsequently be calculated by substituting equation 2 in equation 1, and fitting the resulting equation by non-linear regression to observations on annual transgression frequencies of different elevations. In our case, transgression frequencies were measured for 5-cm elevational classes, and the model fitted very well ($r^2 = 0.99$, $n = 169$). The parameter values for b and c might be obtained from sedimentation experiments with simultaneous measurement of transgression frequencies. In our case, however, these parameters were not measured independently, but calibrated to the observed silt-layer thickness after 10, 25, 35, 60, 100 and 200 years, at different base elevations (every 10 cm for each transect). In addition to the measured data, we added points at 0.2, 0.3, 0.4 and 0.5 m NAP, with zero sedimentation, since sedimentation was never observed at this low elevation in the field. Adding these points made it much easier to calibrate the model to the field data. The calibration was done by solving the model starting with an initial guess of b and c, evaluating the sum of the squared differences between observed and predicted values, and subsequently adjusting b and/or c until this residual sum of squares was minimal. The Solver procedure from Microsoft Excel 6.0 was used to find a best combination for b and c, using automatic scaling, quadratic extrapolation and forward differencing. The R^2 of the regression between observed and predicted values for the solution was 0.86 ($n = 116$).

Using these statistical procedures, we obtained the following parameter values for the Schiermonnikoog salt marsh:

a	5.648	relative decrease in annual transgression frequency with increasing elevation (m above NAP), indicating the temporal variance in high tide level;
b	7.97E-05	linear coefficient for the dependence of annual sedimentation rate (m) on annual transgression frequency, related to tidal amplitude and sediment load;
c	1.63E-02	exponential coefficient for the dependence of annual sedimentation rate (m) on annual transgression frequency, related to tidal amplitude and sediment load;
h_0	0.891	initial annual mean high tide (m above NAP) in 1824 (intercept of the linear regression);
r	6.3×10^{-4}	average annual change in mean high tide (m), indicating sea-level rise, over the period 1824–1993 (slope of the linear regression);
m	706	total number of tides per year (irrespective of elevation).