# Salt marshes along the coast of The Netherlands

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## Abstract

The area of salt marshes does no longer increase. The recent erosion coincides with a rise in MHT-level in the last 25 years. Despite the decrease in area, sedimentation continues, especially in the lower salt marsh, which acts as a sink of nitrogen. Assimilation and mineralization of nitrogen are in balance in most plant communities along the gradient from lower to higher salt marshes. Mineralization of nitrogen increases towards the higher salt marsh, whereas the above-ground production and the mean nitrogen content of plants decrease. There is a positive correlation between quality of food plants in salt marshes and breeding success of Brent geese in the arctic tundra. Sedimentation on mainland salt marshes can compensate for the expected sea level rise. This is not the case for island salt marshes, if the relative sea level rise is more than $0.5–1.0$ cm yr$^{-1}$. The natural succession on salt marshes results in an accumulation of organic material, which is related to the dominance of single plant species. It is not clear to which extent this process is enhanced by eutrophication from acid deposition and seawater. Human exploitation of unprotected salt marshes is old and heavy in the system of mound settlements. Reclamation rates by dikes in the last centuries were higher than the rate of area increase. Grazing by cattle as a management practice results in both a higher plant species-richness and community diversity than abandoning; hay-making is intermediate, but shows less structural diversity than grazing with low stocking density. The invertebrate fauna is favoured by a short period of abandoning, but eventually characteristic salt marsh invertebrates are replaced by inland species. Many bird species prefer grazed salt marshes. The final section gives some perspectives. Provided that no further embankments take place the optimal nature management option for plants and animals is a vegetation pattern, which includes areas with a low canopy (grazed) and areas with a tall canopy.

## System characteristics

### Area increase and sedimentation in salt marshes

Conditions for the formation of salt marshes are best on a gently sloping shoreline with little wave energy and sufficient sediment supply (Dijkema, 1987). Surface elevation, tidal amplitude, and drainage must be sufficient to allow periods of soil aeration necessary for plant growth (Armstrong *et al.*, 1985). Pioneer plants (*Salicornia*

*dolichostachya** and *Spartina anglica*) and further sedimentation create an environment which promotes a closed coverage of perennial halophytic plants. Around Mean High Tide (MHT)-level *Puccinellia maritima* reaches sufficient abundance to enhance maximal sedimentation.

The total area of salt marshes in the Dutch Wadden Sea area is presently 7,300 ha, including 1,900 ha pioneer zone (Dijkema *et al.*, 1990). The average seaward expansion along the mainland coast was 8.2 m yr$^{-1}$ for Friesland and 4.7 m yr$^{-1}$ for Groningen for the period 1960–1985. These rates are similar to those observed in German mainland salt marshes, namely, 7.1 m yr$^{-1}$ for the period 1930–1978 and 4.7 m yr$^{-1}$ for the period 1940–1979 (Dieckmann, 1988). The seaward expansion of the western section of the Friesland mainland coast only took place in recent years (Fig. 1), whereas it was constant for the entire period ($> 1$ m yr$^{-1}$) in the eastern section. Almost all seaward expansion of the central section of Friesland and the western section of the Groningen coast occurred in the 1960's. The marsh area stabilized later on and erosion occurred during the past 10 years. The eastern section of the Groningen coast shows a net reduction in salt marsh area after 1960. The total area of the mainland saltmarshes increased by 1,000 ha in

the period 1960–1978, whereas a reduction of 380 ha took place in the period 1978–1988 (P.Bouwsema, pers.comm.).

Sedimentation was higher from 1960 to 1968, shortly after the construction of the sedimentation fields, than in later years (1968–1987) in the Wadden Sea mainland coastal area. The sedimentation balances differ in the various sections along the coast (Fig. 2). In the sections of west and east Friesland and in west Groningen the balance is positive relative to MHT (0.9–1.7 cm yr$^{-1}$ on average), whereas in the sections of central Friesland and east Groningen a negative balance is found in the pioneer zone ($-0.8$ cm yr$^{-1}$) for the period 1978–1987. The sedimentation is highest between MHT-level (MHT = NAP + 1.25 m) and 20 cm above MHT-level and decreases again at higher elevation due to less frequent tidal flooding, namely, 0.7–2.0 cm yr$^{-1}$ (at NAP + 1.30 m) to 0.6 cm yr$^{-1}$ (at NAP + 2.00 m) in mainland salt marshes and 0.4 cm yr$^{-1}$ (at NAP + 1.30 m) to 0 cm yr$^{-1}$ (at NAP + 2.00 m) in barrier island marshes (Dijkema *et al.*, 1990) (NAP = Nieuw Amsterdams Peil; similar to Ordnance Date).

The sedimentation rate is affected by grazing as demonstrated in the mainland salt marsh of the Leybucht in Germany. In the *Puccinellia maritima*-zone (NAP + 1.40 m) a sedimentation of 2.3 cm yr$^{-1}$ was found in the ungrazed area and 1.7 cm yr$^{-1}$ in the grazed site. No differences were found between grazed and ungrazed sites in the *Festuca rubra*-zone at NAP + 1.8 m (1.6 cm yr$^{-1}$) and in the *Salicornia dolichostachya*-zone at NAP + 1.1 m (1.8 cm yr$^{-1}$) (Andresen *et al.*, 1990).

The recent erosion of salt marshes in the Wadden Sea area might be caused by the increase in MHT-level, namely, 0.44 cm yr$^{-1}$ in the Dutch Wadden Sea from 1960 to 1986, (Dijkema *et al.*, 1990) and 0.46 cm yr$^{-1}$ in the adjacent German Wadden Sea from 1954 to 1986 (Jensen *et al.*, 1988). The higher flooding frequency might eventually result in cliff formation along the salt marshes (Dijkema *et al.*, 1990).

Most estuarine salt marshes in the south-west of the Netherlands are eroding. The high rates of
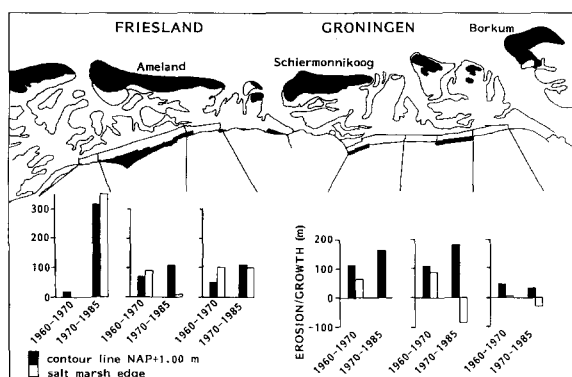


*Fig. 1.* Seaward expansion of the contourline of NAP + 1 m and of the salt marsh edge in the Netherlands Wadden Sea (after Bouwsema *et al.*, 1986).

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* Nomenclature of taxa follows Van der Meijden *et al.* (1983), that of syntaxa Westhoff & Den Held (1969).
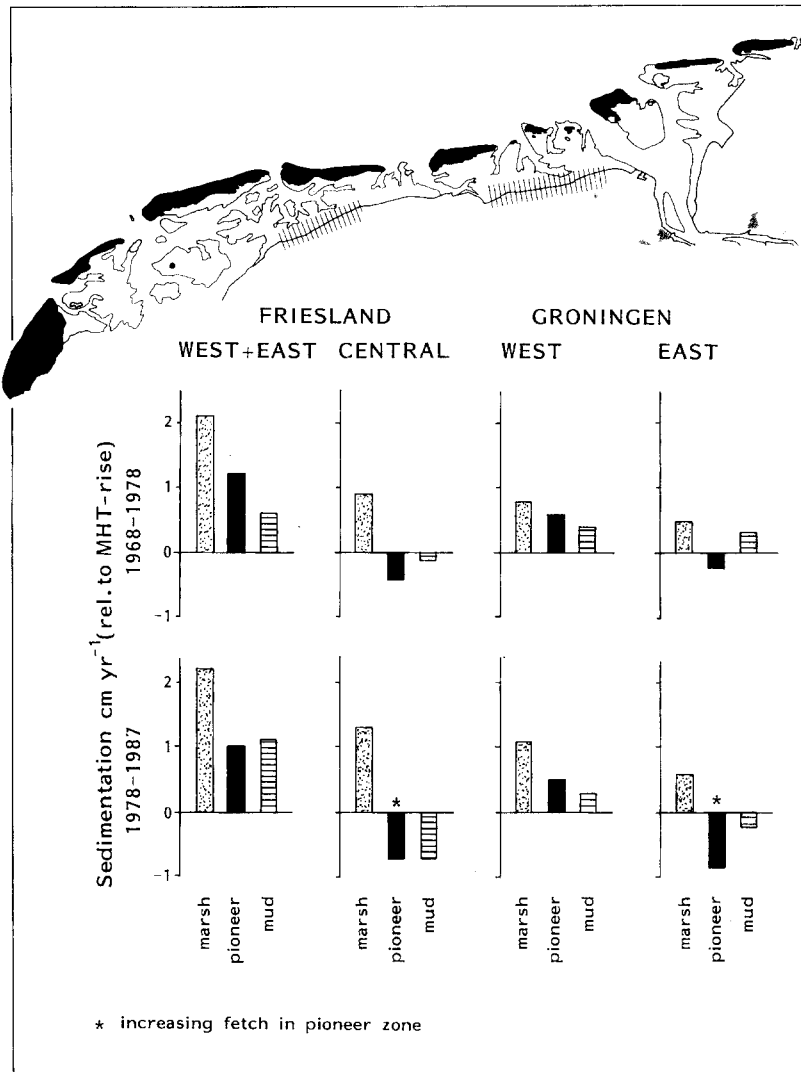
*Fig. 2.* Sedimentation relative to MHT-rise in mainland salt marshes and mud flats in the Netherlands Wadden Sea for the period after the construction of sedimentation fields (after Dijkema *et al.*, 1989).

cliff erosion (up to 4 m yr$^{-1}$) in the eastern part of the Westerschelde have been related to increased tidal stream velocities caused by intensive dredging. The area increase slowed down in the 1930' in the Oosterschelde, and erosion took place over the last decades. The cliff length of the marsh-mud transition increased from 60% in the period 1950 to 1970 to 90% in the early 1980's. This has been attributed to increased tidal amplitude and stream velocities caused by various human activities. The construction of the Oosterschelde storm surge barrier caused a reduction in the tidal amplitude and it was therefore expected that the rate of cliff erosion would decrease. To date, the rate has, however, remained high (De Jong, 1991).

*Geochemical cycles*

*System behaviour*

*Import–export*

Geochemical cycles in salt marshes are open systems due to import and export of large amounts

of organic material and nutrients. Transport of particulate and dissolved matter between salt marshes and the sea takes place by tidal water. Salt marshes are often regarded as sinks for organic material, nutrients and heavy metals since sedimentation of particulate matter takes place. The net direction of transport of materials between salt marshes and the sea is, however, complicated. In several studies different methodological approaches have been applied to estimate the net exchange and the variation in results can partly be ascribed to the approach used, especially with respect to the hydrographical balance (Wolaver et al., 1983; Dankers et al., 1984). Much of the variability among various marshes may be due to factors related to geographic position, marsh morphology and hydrology (Whiting et al., 1987).

Phosphate is generally exported from the salt marsh on an annual basis, whereas organic phosphorus is imported (Jordan et al., 1983). In the Dutch Ems-Dollard estuary also a small export of phosphate of 2.8 kg P ha$^{-1}$ yr$^{-1}$ was found (Dankers et al., 1984). A net overall export of nitrogen, ranging from 7 to 111 kg N ha$^{-1}$ yr$^{-1}$ is often found (Rozema & Leendertse, 1991). The role of salt marshes in the nitrogen cycle is mainly that of nitrogen processor since oxidized forms, like nitrate, are generally exported, and reduced forms, like ammonia and dissolved organic nitrogen, are imported (Abd. Aziz & Nedwell, 1986). In a mesohaline marsh, in contrast, a large annual import of nitrogen was found (Wolaver et al., 1983). The annual import of nitrate in and export of ammonia out of the Ems-Dollard salt marsh as measured by Dankers et al. (1984) is in agreement with the conclusions of Abd. Aziz & Nedwell (1986). The large input of particulate matter in the Ems-Dollard salt marsh could, however, mean an input of particulate nitrogen into the marsh and hence a net input of nitrogen.

Many authors suggest that the quantification of nitrogen fluxes during storm tides may be important for the annual balance, but such measurements are rarely done because of practical problems. Dankers et al. (1984) estimated the export of coarse debris during storm tides to be low as

compared to the primary production of the salt marsh.

## Effects of age of salt marshes

Valiela & Teal (1979) expected that relatively old salt marshes, like at their study site, eventually reach a steady state in which the import and export of nitrogen are nearly balanced. Relatively young marshes like those in the Wadden Sea may, therefore, act differently i.e. as a sink for nitrogen as a whole (Leendertse, 1989).

## Effects of zonation of plant communities

The objective of transport studies such as the afore-mentioned is to quantify the import and export for a whole salt marsh. They consist, however, of different plant communities according to the abiotic zonation. To understand the mechanisms of the production and decomposition phenomena of salt marshes, it is necessary to have knowledge of the plant community level. Jordan et al. (1983), for example, found differences in the annual nitrogen budget of higher and lower parts of a brackish salt marsh, namely, a net import of 9 kg N ha$^{-1}$ yr$^{-1}$ in the lower marsh and a net export of 28 kg N ha$^{-1}$ yr$^{-1}$ in the higher marsh.

## Nitrogen cycle

### Net exchange between salt marsh and sea, assimilation, decomposition and mineralization

Nitrogen plays an important part in the functioning of salt marshes. It can control processes like the productivity of primary and secondary producers, and of decomposition rates of organic material (Teal, 1986). This became clear from a study of the N cycle of the Great Sippewisset Marsh (USA). N was imported by sea water, dry and wet deposition, groundwater, sedimentation and fixation. It was exported by sea water and denitrification. Considerable assimilation and

mineralization occurred in the marsh itself. A British study on the annual cycling of nitrogen in a *Puccinellia maritima* community indicated, for instance, that assimilation (225 kg N ha$^{-1}$ yr$^{-1}$), and decomposition and mineralization (195 kg N ha$^{-1}$ yr$^{-1}$) were high compared to the net import and export (7 kg N ha$^{-1}$ yr$^{-1}$), but about half as high as the total import and export (500 kg N ha$^{-1}$ yr$^{-1}$), while aerial deposition was considered negligible (Fig. 3; Abd. Aziz & Nedwell, 1986).

Mineralization usually outweighs humification in salt marshes (Beeftink, 1966). This is illustrated by the following calculations. The soil nitrogen pool of sandy and clay-rich salt marshes in northern Germany ranged from 5,000 to 12,000 kg ha$^{-1}$; humus accumulation from 1,700 to 12,400 kg ha$^{-1}$ (sedimentation rate of 1 cm yr$^{-1}$ assumed; Scherfose, 1987). The N mobility, i.e. the ratio mineral N: total N, in salt marshes is high (2.6 to 8.7%; Scherfose, 1987) compared to that in inland ecosystems (1 to 4%; Alexander, 1977).

*Aerial deposition*

Although aerial deposition was considered negligible (Abd. Aziz & Nedwell, 1986), it can be considerable, at least 43 kg N ha$^{-1}$ yr$^{-1}$ (22 kg NO$_x$ and 21 kg NH$_y$ ha$^{-1}$ yr$^{-1}$) in the Netherlands in 1987 (Additioneel Programma Verzuringsonderzoek, 1989). If this deposition had been the same

in the British study, it would have accounted for 22% of the mineralized nitrogen in the *Puccinellia maritima* community.

*Hay-making and grazing*

The removal of nitrogen by hay-making and grazing is often not taken into account in many budget studies. The amount of nitrogen removed by hay-making on the island of Schiermonnikoog can range from 16 to 131 kg N ha$^{-1}$ yr$^{-1}$ in various plant communities (Table 1). The export of nitrogen by grazing, however, cannot merely be derived from the utilized biomass, since utilization includes both foraging and trampling. Foraging can amount to 30% of the herbage utilized by cattle and 50% for that by geese (Looijen & Bakker, 1987). This implies that the amount of nitrogen removed by grazing ranges from 10–70 kg N ha$^{-1}$ yr$^{-1}$ for the combined effects of cattle and geese-grazing (Table 1). Thus, going back to the British study (Abd. Aziz & Nedwell, 1986) cattle can remove about 40 kg N ha$^{-1}$ yr$^{-1}$ and geese 30 kg N ha$^{-1}$ yr$^{-1}$ from a *Puccinellia maritima* community.

Nitrogen is not removed by herbivores, but in fact reallocated. It reaches the soil again as dung and contributes as such to the nitrogen cycle. The mineral cycling of nitrogen, can even up to tenfold be stimulated (Floate, 1970). The above-ground plant biomass was demonstrated to increase by geese-grazing, possibly due to the rapid recycling of nitrogen from faeces (Fig. 4; Hik & Jefferies, 1990).

*Balancing items of nitrogen budgets*

Mineralization of nitrogen strongly varies with zonation and different plant communities (Table 2; Scherfose, 1987), and generalization of data is therefore risky. The nitrogen assimilation and mineralization in the British *Puccinellia maritima* community (Abd. Aziz & Nedwell, 1986), a Danish *Halimione portulacoides* community (Henriksen & Jensen, 1979) and a German *Festuca*



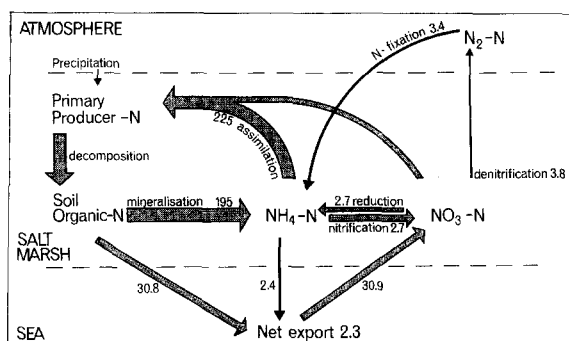*Fig. 3.* The annual nitrogen budget for a *Puccinellia marritima* community in eastern England. Fluxes of nitrogen are shown as kg N ha$^{-1}$ yr$^{-1}$ (after Abd. Aziz & Nedwell, 1986).

*Table 1.* The removal of plant nitrogen by hay-making and grazing, calculated from the mean biomass removed by anual cutting, the biomass utilized by cattle and geese, and the mean nitrogen contents of the plant communities. Biomass utilization by grazing was measured as the difference between herbage under exclusion cages and in open plots according to Looijen & Bakker (1987). Trampling effects were estimated as 70% of utilization by cattle and 50% of utilization by geese (Looijen & Bakker, 1987). –: not measured.

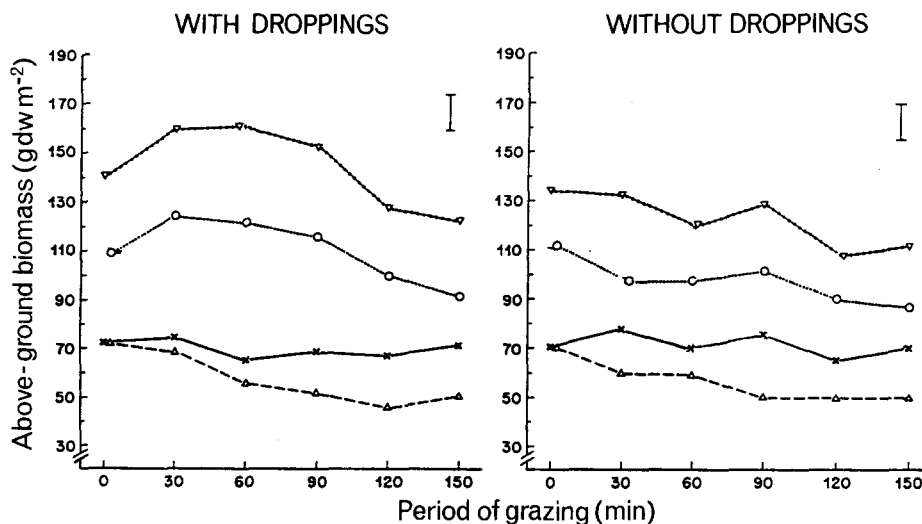| Plant community Schiermonnikoog The Netherlands | Hay-making | | Cattle grazing | | Geese grazing | | Mean nitrogen content (%) | Total grazing corrected for trampling. Nitrogen removed kg ha$^{-1}$ yr$^{-1}$ |
|---|---|---|---|---|---|---|---|---|
| | Mean biomass removed (g m$^{-2}$) | Nitrogen removed (kg ha$^{-1}$ yr$^{-1}$) | Biomass utilized (g m$^{-2}$) | Nitrogen removed (kg ha$^{-1}$ yr$^{-1}$) | Biomass utilized (g m$^{-2}$) | Nitrogen removed (kg ha$^{-1}$ yr$^{-1}$) | | |
| *Puccinellia maritima* | – | – | 415 | 145 | 181 | 63 | 3.5 | 70 |
| *Juncus gerardii* | 311 | 84 | 174 | 47 | 38 | 10 | 2.7 | 18 |
| *Festuca rubra* | 273 | 55 | 144 | 29 | 75 | 15 | 2.0 | 15 |
| *Armeria maritima* | 113 | 16 | 229 | 32 | – | – | 1.4 | 10 |
| *Juncus maritimus* | 355 | 60 | 1054 | 180 | – | – | 1.7 | 60 |
| *Elymus pycnanthus* | 266 | 38 | – | – | – | – | 1.4 | – |
| *Artemisia maritima* | 413 | 131 | – | – | – | – | 3.2 | – |



*Fig. 4.* The above-ground plant biomass after different periods of grazing with droppings left and with the droppings removed (after Hik & Jefferies, 1990).

*rubra* community (Zimmek, 1975) balance more or less. A shortage of mineralized nitrogen was, however, estimated in a German *Puccinellia maritima* community which was possibly replenishned by bird droppings and groundwater from the higher parts of the marsh (Zimmek, 1975). The nitrogen assimilation by roots was quantified in the British *Puccinellia maritima* community (Abd. Aziz & Nedwell, 1986). This might be important for the balance between mineralization and as-

similation, but it is not clear whether it is taken into account in the other studies.

## Heavy metals

The exchange of heavy metals between sea and salt marsh has not been measured as intensively as the exchange of nutrients. The retention of heavy metals is mainly due to the anoxic soil con-

Table 2. Standing crop, including accumulated litter, of salt marsh plant communities and the mineralization and decomposition rates in different salt marsh zones and a beach plain. (1) Groenendijk, 1987. (2) Henriksen & Jensen, 1979; (3) Abd.Aziz & Nedwell, 1979; (4) Zimmek, 1975; (5) Scherfose, 1987; (6) Rozema, 1978; (7) Bakker, 1989; (8) Looijen & Bakker, 1987. –: not measured.

| Salt marsh zone | Plant community | Inundation frequency (N yr$^{-1}$) | Standing crop + litter (gwd m$^{-2}$) | Net mineralization rate (kg N ha$^{-1}$) | | Decomposition rate (% cellulose disappeared) Per growing season |
|---|---|---|---|---|---|---|
| | | | | Per year | Per growing season | |
| Pioneerzone | Salicornia europaea | 350–600 | – | – | 50 (5) | – |
| | Spartina anglica | 350–600 | 970 (1) | | 35 (5) | – |
| Lower salt marsh | Puccinellia maritima | 130–350 | 360 (1) | 195 (3); 50 (4) | 60 (5) | 96 (8) |
| | Halimione portulacoides | 130 | 1300 (1) | 110 (2) | 90 (5) | – |
| Mid salt marsh | Juncus gerardii | 40 | 400–800 (7) | – | 70 (5) | 76 (8) |
| | Artemisia maritima | 30–160 | 1100–1300 (7) | – | 110 (5) | – |
| Upper salt marsh | Juncus maritimus | 12–60 | 800–1500 (7) | – | 75 (5) | 93 (8) |
| | Elymus pycnanthus | 20–40 | 1300–1500 (7) | – | – | – |
| | Festuca rubra | 12–30 | 400–1000 (7) | 150 (4) | 100 (5) | 58 (8) |
| | Armeria maritima | 30–80 | 200–400 (7) | – | 55 (5) | 15 (8) |
| Beach plain | | 2–5 | – | 15 (6) | – | – |

ditions in salt marshes. The sediments contain high levels of sulfide under reduced conditions and lead-, zinc-, copper- and cadmium-ions form insoluble and relatively stable sulfides under these conditions. Budget studies for lead and cadmium were carried out by applying contaminated fertilizers to the salt marsh and estimating the retention (Banus et al., 1975). Lead and cadmium were largely retained in the salt marsh soil (96% and 35–80%, respectively). Other data included retention of 20–35% for cadmium, 20–50% for chrome and 20–45% for zinc (Giblin et al., 1983). The oxidation of the soil by plant roots may reduce its retention for heavy metals. The exchange of heavy metals between sea and salt marsh will also depend on the amount of metals taken up by plants and animals. Transport of metal-containing plant material to the sea means export from salt marsh sediments.

*Original and unexploited plant communities*

The tidal marsh landscapes which formerly extended all along the whole Dutch coast have changed dramatically in (pre)historic times. The investigation of plant remains such as pollen and macro-fossils from prehistoric settlements yielded evidence concerning these habitats.

Habitats far from the sea were supplied with fresh water from the hinterland. A continuous sea level rise took place from the last glacial period onwards. Natural drainage became blocked and an extensive accumulation of organic material took place as far as the fringes of the Pleistocene cover sands. Both fen-peat (*Magnocaricion, Phragmition, Alnion glutinosae*) and bog-peat (*Sphagnion, Ericion tetralicis*) developed, depending on the regional and local hydrology (Fig. 5). Most peat was covered by clay during transgression periods, vast areas from the middle ages onwards (Behre, 1979). One example of peat which has not been covered, is located outside the dike and is therefore floating, is in the Jadebusen in Germany (Schwimmendes Moor) (Wiermann, 1965; Luck, 1976). River bank forests (*Fraxino-Ulmetum*) have been recorded from the early sub-boreal period (ca. 4500 B.C.) until the Iron Age (ca. 500 B.C.) on the elevated levees deposited by water along the lower parts of rivers, for instance
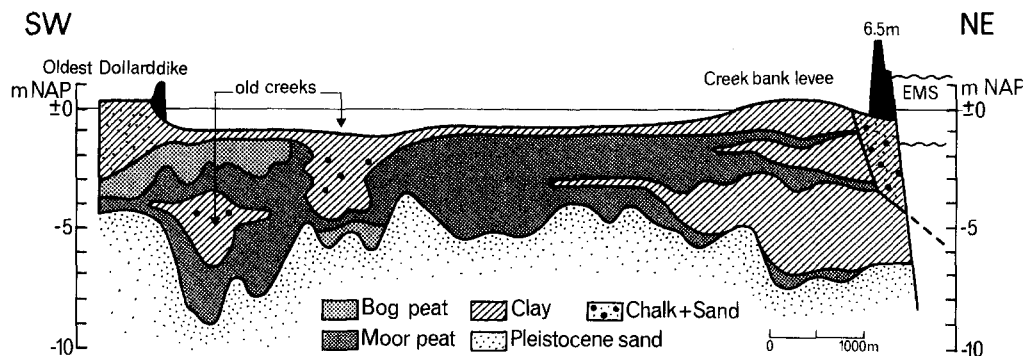
Fig. 5. Transect through the marshes between the river Ems and the Dollard in north-west Germany (after Behre, 1979).

the Ems in Germany. Mainly *Phragmition* and *Bidention* communities and some *Magnocaricion* occurred in the neighbourhood of the levees in the period from 700 B.C. until 300 A.D. as examples of natural treeless communities (Behre, 1979).

The transition zone between fresh and salt tidal water landscapes must have been represented by plant communities indicating brackish conditions. Indeed brackish elements of fresh water *Phragmition* communities (especially *Scirpus maritimus*) and of salt water *Armerion maritimae* communities (especially *Eleocharis palustris* ssp. *uniglumis*) have been found (Behre, 1979).

All the aforementioned plant communities were not protected by dikes. Salt marsh communities are the only unprotected ones at present. In order to understand the synecology of the former salt marsh plant communities, they are based on the present knowledge of plant communities. Starting from the tidal flats, a characteristic zonation in the natural halosere of salt marsh communities is found on the sandy barrier islands of the Wadden Sea (Westhoff & Den Held, 1969; Beeftink, 1977A; Dijkema, 1983). The *Salicornietum strictae* and *Spartinetum townsendii* occur on tidal flats with daily submergence in the pioneer zone. The lower salt marsh, between mean high water (MHW) and spring tide level is characterized by the *Puccinellion maritimae* with the *Puccinellietum maritimae* in depressions, the *Halimionetum portulacoidis* on creek bank levees and the *Plantagini-Limonietum* in the intermediate positions. The *Armerion maritimae* occurs on the mid and upper

salt marsh from just below the spring tide level up to the level reached by winter storm floods. The *Juncetum gerardii* is found on the clay soils, whereas the *Artemisietum maritimae* occurs on sand ridges and creek bank levees. The *Puccinellio-Spergularion salinae* community can develop in places with irregularly changing conditions such as occasionally stagnant water. The *Atriplici-Agropyretum pungentis* can develop higher on the salt marsh after the deposition of drift material. *Lolio-Potentillion* communities can be found on the upper slightly desalinated salt marsh (communities of *Agrostis stolonifera* and *Trifolium fragiferum*) and on adjacent low dunes (community of *Ononis spinosa* and *Carex distans*). A more ephemeral community can also be found at the transition of wet/salt and dry/fresh, viz. the *Saginion maritimae*. The relationship of the halosere on mainland salt marshes to the inundation frequency is shown in Fig. 6.

*Plant biomass characteristics*

The above-ground standing crop shows a large variation in the different plant communities over the salt marsh zones and from year-to-year (Table 2). These differences can partly be attributed to various amounts of accumulated litter in the biomass samples. Since the standing crop and the amount of litter depend on the relative rates of production and decomposition, it seems necessary to focus on these processes.
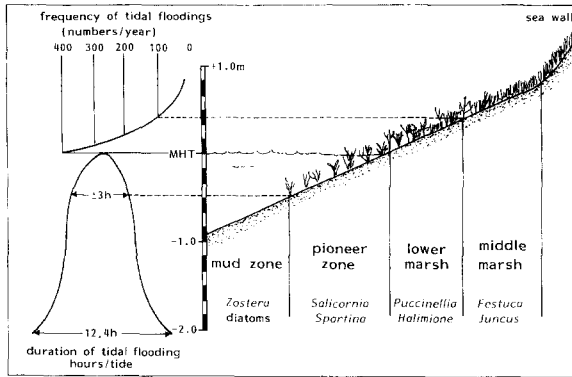
*Fig. 6.* Zonation of mainland salt marshes in relation to duration and frequency of tidal floodings (after Erchinger, 1985).

The primary production in salt marshes is extremely high. Above-ground production in Dutch salt marshes varies widely: from 300–400 g m$^{-2}$ in *Juncus gerardii* and *Festuca rubra* communities on higher salt marshes in the Wadden Sea area to over 1,500 g m$^{-2}$ in *Spartina anglica* stands on low marshes in the south-west of the Netherlands and in *Juncus maritimus* communities on Schiermonnikoog (Table 3). This suggests a generally negative relationship between the above-ground production of salt marsh plant communities and their frequency of inundation (Table 3).

A high spatial and temporal variation within plant communities is, however, found. A large range (100–1,000 g m$^{-2}$) in production estimates was found in *Spartina anglica* communities in the south-west of the Netherlands (De Leeuw & Buth, 1991). Large year-to-year fluctuations in standing crop occurred on Schiermonnikoog (in the northern Netherlands) in annually cut areas in various plant communities on the mid- and high-salt marsh with no litter present (De Leeuw et al., 1990). These communities showed, however, a synchronous pattern in peak above-ground biomass over a 13-year period. These fluctuations could be explained by the rainfall deficit in the growing season, but not by the inundation frequency (Fig. 7). The soil salinity was positively and the soil moisture content was negatively cor-

*Table 3.* Annual above-ground, below-ground and the ratio below-gr.: above-gr. production for Dutch salt marsh plant communities. Above-ground production estimated according to Smalley, 1959; below-ground production according to the change in biomass technique (Dahlman & Kucera, 1965). (1) Groenendijk, 1984; (2) Groenendijk & Vink-Lievaart, 1987; (3) Ketner, 1972; (4) Looijen & Bakker, 1987; Wolff et al., 1980; (6) A. Fuchs, unpubl.

| Salt marsh zone | Plant community | Locality | Above-ground production (gwd m$^{-2}$ yr$^{-1}$) | Below-ground production (gwd m$^{-2}$ yr$^{-1}$) | Ratio Below-gr. above-gr. |
|---|---|---|---|---|---|
| Pioneerzone | *Spartina anglica* | Oosterschelde | 1650 (1) | 6044 (2) | 3.7 |
| | *Spartina anglica* | Oosterschelde | 1057 (6) | | |
| | *Spartina anglica* | Oosterschelde | 1030 (5) | | |
| Lower salt marsh | *Puccinellia maritima* | Schiermonnikoog | 767 (4) | | |
| | *Puccinellia maritima* | Terschelling | 497 (3) | | |
| | *Puccinellia maritima* | Oosterschelde | 992 (6) | | |
| | *Puccinellia maritima* | Oosterschelde | 837 (5) | | |
| | *Halimione portulacoides* | Oosterschelde | 1400 (1) | 7977 (2) | 5.7 |
| | *Halimione portulacoides* | Oosterschelde | 575 (6) | | |
| Mid salt marsh | *Triglochin maritima* | Oosterschelde | 70 (1) | 3475 (2) | 5.0 |
| | *Plantago maritima* | Terschelling | 514 (3) | 1138 (3) | 2.2 |
| | *Juncus gerardii* | Terschelling | 344 (3) | 601 (3) | 1.7 |
| | *Juncus gerardii* | Schiermonnikoog | 429 (4) | | |
| Upper salt marsh | *Elymus pycnanthus* | Oosterschelde | 900 (1) | 4421 (2) | 4.9 |
| | *Elymus pycnanthus* | Oosterschelde | 1008 (5) | | |
| | *Festuca rubra* | Schiermonnikoog | 388 (4) | | |
| | *Juncus maritimus* | Schiermonnikoog | 1707 (4) | | |
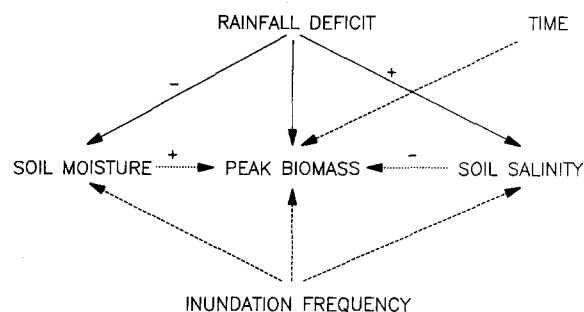
*Fig. 7.* Factors affecting peak biomass accumulation; ———— = significant correlation, ------- = no significant correlation, ········ = suggested relation (after De Leeuw *et al.*, 1990).

related with the rainfall deficit in a two-year period in these mid- and high-salt marsh communities. The production of lower salt marsh ecosystems, in contrast, is probably not affected by the rainfall deficit during the growing season (De Leeuw *et al.*, 1991).

Below-ground production generally outweighs above-ground production in salt marshes. It also varies widely: from 300–1,000 g m$^{-2}$ (Ketner, 1972) to 3,500–8,000 g m$^{-2}$ (Groenendijk, 1987). The high below-ground production estimates in the Oosterschelde estuary (Table 3) are similar to those reported from north American marshes (Groenendijk, 1987).

The question arises why lower salt marsh halophytes, in particular, invest so much in below-ground production. It was demonstrated that the above-ground production of several *Spartina alterniflora* marshes varied widely, whereas the below-ground production remained nearly constant (Teal, 1986). A larger part of the total production was invested below-ground in low productive marshes than in high productive ones. The grass might first allocate sufficient assimilates to below-ground structures to gain the nutrients required and subsequently invests the excess into photosynthetic parts (Teal, 1986). The data in Table 3 show, in contrast, the opposite. The plant communities with the higher above-ground production studied by Groenendijk (1987) invested a larger proportion of the total production into below-ground structures than the lower produc-

tive communities studied by Ketner (1972). Reason for this may be that the roots of the salt marsh species have other functions apart from the acquisition of nutrients. They anchor the plants in the sometimes unstable sediments and protect the substrate from erosion (Van Eerdt, 1985). It may be assumed that the latter function of roots is more important in the lower than in the higher salt marsh.

High decomposition rates in salt marsh ecosystems have been reported from both the Wadden Sea area (Table 2) and the south-west of the Netherlands (Hemminga & Buth, 1991). Decomposition rates (% weight loss day$^{-1}$) estimated with litter bag techniques for different plant parts of a number of salt marsh species in the southwest of the Netherlands varied between 0 and 0.55%. These data were used to obtain a ranking of factors according to the extent in which they induce variations in the rates of decomposition. Tissue composition was the most important factor in the explanation of this variation, in particular the content of lignin in different plant parts and species. Environmental heterogeneity came next, while the decomposition stimulating effect of the larger macrofauna was the least important factor. The effects of a number of environmental variables was studied using the cotton strip method. The water, silt and salt content of the soil and the coverage by the vegetation were most important. Fifty-one and 56% of the variance in loss of tensile strength of the strips in respectively spring and summer was explained by these factors (Hemminga & Buth, 1991).

## Geese grazing: from salt marshes to the arctic tundra

The relationship between Brent geese and food plants in the spring staging area, and their breeding success in the arctic tundra, is shown in Fig. 8.

The preference of geese for grazed salt marshes can be attributed to the quality of forage i.e. the high ratio of green to dead biomass in the *Puccinellia maritima*, the *Juncus gerardii* and the *Festuca rubra* communities (Bakker, 1989). De-
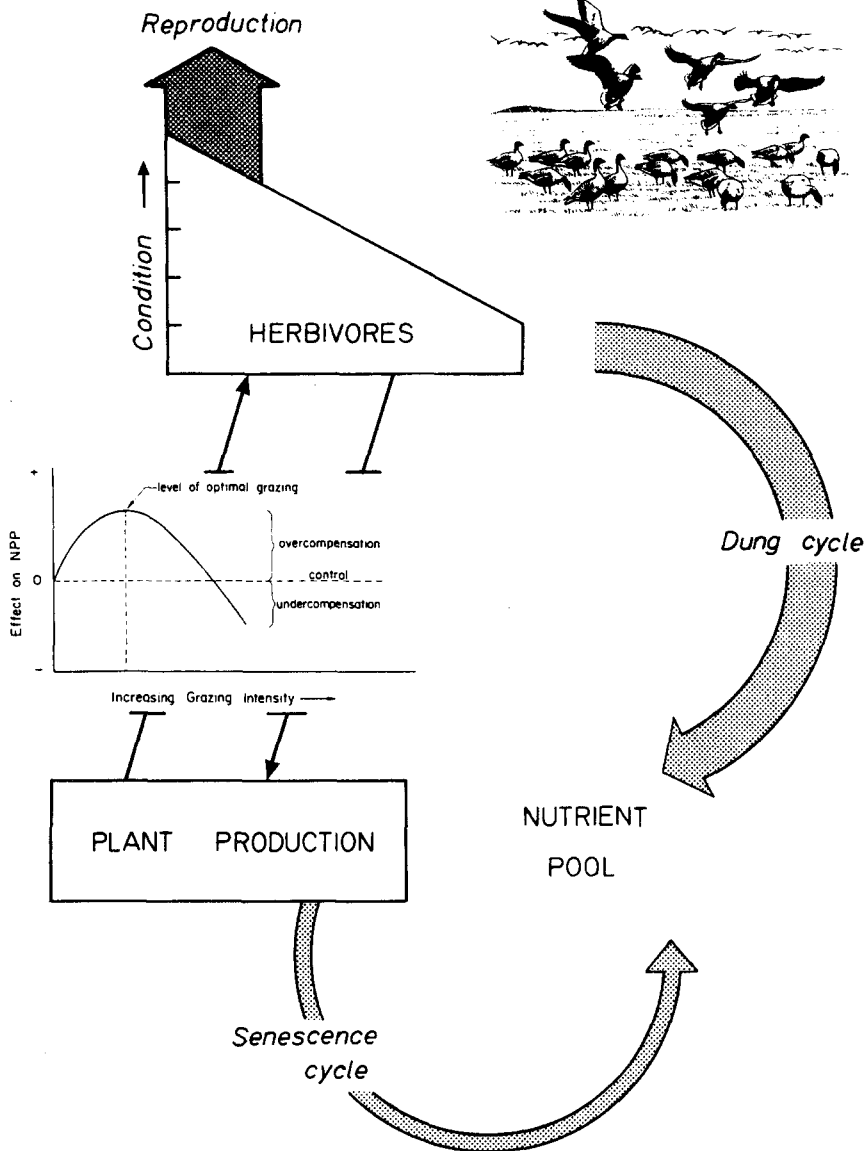
*Fig. 8.* Flow diagram of herbivore/plant interactions according to the grazing optimization hypothesis (NNP = net above-ground primary production). The relative importance of the dung cycle as contrasted to the return of nutrients via senescence, is symbolized by the thickness of the arrows.

tailed measurements revealed a nitrogen content of 4.2% in *Festuca rubra* in February, of 4.2% in Barnacle geese-grazed and of 3.2% in ungrazed plants until the end of April, suggesting that grazing kept the nitrogen content higher in grazed than in ungrazed plants and that geese so to speak manipulate the quality of their food supply by repeated grazing (Drent & Prins, 1987).

The food quality in the spring staging areas in the salt marshes is important since they serve as a source to gain weight before migration and to hatch their young. Successful parents of Barnacle geese, i.e. females accompanied by young in the autumn had a higher body mass before departure in the spring than unsuccessful parents (Ebbinge *et al.*, 1982). The share of juveniles in the total population in a year-to-year comparison increase with increasing food quality (Drent & Prins,

1987). Food supply, which depends on the position of individuals in the flock, also influenced the yearly breeding success of individual Brent geese. Goose visitations of the salt marsh of the island of Schiermonnikoog followed a pulsating pattern with massive visits every 3–5 days (Prins *et al.*, 1980). Each flock visit the entire harvestable fraction was removed and it was demonstrated that the birds at the rear of the flock already faced a heavily depleted food supply, especially of the preferred food plant in this zone, *Plantago maritima*. The reason for the strong preference for this species over the alternative food plant (*Puccinellia maritima*) is the far higher harvesting potential for geese. It was demonstrated that half of all *Plantago* feeding time was spent by only 12% of the birds, whereas 27% of the birds obtained no *Plantago* at all and had to feed on *Puccinellia* (Drent & Prins, 1987).

## Threats

### *Effects of sea level rise and climatic change*

#### *Sea level rise*

The relative sea level rise in the Wadden Sea area consists of several components. The eustatic sea level rise is 0.10–0.12 cm yr$^{-1}$ over the period 1880–1980 (Gornitz & Lebedeff, 1987), the local tectonic subsidence is estimated at 0–0.04 cm yr$^{-1}$ over the period 1926–1987 (P. Noomen, in prep.). Subsidence due to gas extraction along the Groningen coast was 0.1–0.2 cm yr$^{-1}$ over the period 1964–1987. The mean relative sea level rise, calculated from the eustatic sea level rise and the tectonic subsidence can be estimated at 0.10–0.16 cm yr$^{-1}$. This value is somewhat smaller than that registered by tide gauges for the Dutch Wadden Sea over the period 1933–1980, viz. 0.15–0.17 cm yr$^{-1}$ (Van Malde, 1984). In an other section on sedimentation in salt marshes, the rise of MHT level of 0.44 cm yr$^{-1}$ was mentioned, but that rise is independent of the relative sea level rise.

The problem in predicting the survival poten-tial of salt marshes regarding the future sea level rise lies in the uncertainty of the expected rise value. The globally expected eustatic mean sea level rise is 0.5 cm yr$^{-1}$ until the year 2025, but the standard deviation equals the expected rise (J.Oerlemans, in Dijkema *et al.*, 1990). Moreover, there are no predictions of future MHT levels. One has to reckon with an extra subsidence of 0.1–0.6 cm yr$^{-1}$ until 2025 for the Groningen coast and of 0.8–1.5 cm yr$^{-1}$ for the island of Ameland as a result of gas extraction. The MHT rise has to be considered in relation to both the salt marsh zone itself and to the tidal flat transition in front of it. It seems that the potential loss of salt marsh area through erosion from the seaward edge does not depend on the sedimentation processes on the salt marsh itself, but on that in the pioneer zones in front of the marsh (Dijkema *et al.*, 1988; Boorman *et al.*, 1989).

#### *Erosion*

Sea edge erosion may be expected for more than half of the Dutch man-made salt marshes. It will result in large scale cliff formation, provided that the present sedimentation deficit in the pioneer zone continues. Cliffs show a horizontal retreat of 0.02–0.4 m yr$^{-1}$ along the Groningen foreland, 1.9 m yr$^{-1}$ along the Ems estuary (De Glopper, 1981), and 6 m yr$^{-1}$ on mainland salt marshes in Germany (Erchinger, 1987). All barrier islands in the Wadden Sea have a mean cliff erosion of 0.5 m yr$^{-1}$ (Ehlers, 1988).

#### *Sedimentation*

The present sedimentation rate on mainland salt marshes is high enough to compensate for a future relative sea level rise of 1–2 cm yr$^{-1}$, which is more than the expected global sea level rise. This is not true for the higher marsh zones which have a lower sedimentation rate. The sedimentation rate will, however, increase as a result of the increase in the number of tidal floodings due to a sedimentation deficit to that typical of the lower

marsh zone (De Glopper, 1981; Bouwsema *et al.*, 1986). An increased sea level rise will, therefore, probably not affect the mainland salt marshes by regressive succession, i.e., that the plant communities of the higher salt marsh will be replaced by communities of the lower marsh zone.

The barrier island type of salt marshes in the Wadden Sea area will eventually disappear if the relative sea level rise is more than 0.5–1.0 cm $yr^{-1}$. However, there is some evidence for a balance between the present MHT rise of 0.44 cm $yr^{-1}$ and sedimentation within these marshes (Dijkema *et al.*, 1990).

At a long-term sedimentation deficit in the marsh zone as a result of the sea level rise, the survival of the salt marsh depends on the response of the vegetation to the increase in frequency and duration of floodings. For instance regressive succession to plant communities of lower salt marsh zones or to bare tidal flats would locally occur on the barrier island of Ameland, even if the increased sedimentation is taken into account (Dankers *et al.*, 1987). Sedimentation may, however, increase during years with raised MHT levels due to a delay in the regressive succession of the vegetation and thus may compensate for (part of) the sea level rise (Dijkema *et al.*, 1990). More insight is needed on the sedimentation balance and vegetation dynamics in the pioneer zone as a function of year-to-year fluctuations in MHT, wave energy levels, vegetation structure, drainage, and soil fertility. The process of sedimentation itself as well as its effects upon the succession on sites with low and high sedimentation rates should be studied.

*Climatic change*

Anthropogenic impact on the global atmosphere results in an increase of $CO_2$, and possibly temperature and ultra-violet radiation. Specific effects on salt marsh plants can be the following. The increase in atmospheric $CO_2$ will generally favour carbon assimilation of C3-species (Brouns, 1988; Rozema *et al.*, 1991). Interaction with salinity is to be expected in such a way that salt

marsh plants will improve their water use efficiency and will tolerate higher levels of salinity.

The expected rise in temperature will, however, be primarily more advantageous to C4-species, *e.g. Spartina anglica* in Dutch coastal salt marshes and *Spartina maritima* in southern Europe.

Increased UV-B radiation will adversely affect many plant species in salt marshes, dicotyledons perhaps more severely than monocotyledons. The combined effects of global change factors have to be studied intensively in the near future.

*Eutrophication and toxification*

*Natural and cultural eutrophication*

The succession towards dominance of one or few plant species on various sites over the salt marsh zones can be a result of natural eutrophication i.e. the accumulation of litter and the subsequent decomposition and mineralization of the organic material. Eutrophication of the salt marsh by atmospheric deposition and flooding water may accelerate this process.

Severe nutrient loading has occurred in salt marshes during recent decades originating from anthropogenic activities. It is estimated that 208,000 tons of nitrogen and 18,500 tons of phosphorus enter the Dutch Waddens Sea every year (Van Meerendonk *et al.*, 1988). The Scheldt estuary has an annual load of 9,500 tons of nitrogen and 790 tons of phosphorus (Nienhuis, 1989; Herman *et al.*, 1991). The water of the western Wadden Sea contained three times more phosphorus in 1970 than in 1950 (De Jonge & Postma, 1974). It can, therefore, be expected that salt marshes in both the Wadden Sea and Westerschelde are confronted with increased amounts of nutrients brought in by tidal waters (Leendertse, 1989).

Atmospheric deposition of nitrogen has also increased greatly in the last decades: it presently amounts to 43 kg N $ha^{-1} yr^{-1}$ (Additioneel Programma Verzuringsonderzoek, 1989).

The application of nitrogen (the limiting factor) fertilizers usually increases the production of the

vegetation and decreases the number of plant species (Tyler, 1976; Beeftink, 1977B; Jefferies & Perkins, 1977; Valiela, 1984; Asjes, 1988). The application of fertilizers and grazing on a higher salt marsh will eventually cause the replacement of halophytic plant communities by common inland communities (Bakker, 1989).

The increased nitrogen input might accelerate the spread of fast growing plant species, and eventually facilitate their dominance in unexploited sites: *Elymus pycnanthus* on salt marshes and *Calamagrostis canescens* in beach plains. The mechanisms behind this acceleration are yet unknown. To predict the effects on salt marshes of nutrient input by sediments as a result of sea level rise, of an envisaged reduction in the nutrient input from atmospheric deposition and of nutrients dissolved in sea water, and of the impact of management regimes like grazing and cutting, scenarios have to be developed. These scenarios should include the existing knowledge on the balance of organic matter and nutrients and the subdivision over different compartments in various plant communities over the zonation, and can be used to estimate the effects of changes in various factors incorporated in these scenarios.

*Toxification*

Salt marsh plants take up heavy metals from the soil (Beeftink *et al.*, 1982). The uptake differs between species and is also strongly influenced by soil conditions like pH, redox potential and sulfide content. So far no obvious effects of heavy metals on production and germination in salt marsh plants have been found in Dutch field studies (Huiskes & Rozema, 1988).

**Management**

*Human exploitation of the unprotected coastal area*

People living at the fringes of the Pleistocene Plateau in the northeastern part of the Netherlands, in territories adjacent to navigable parts of little

rivers which flowed into the coastal areas, are assumed to have been the first to exploit the salt marshes. Competition between the arable and pastoral component of the agricultural system might have arisen due to sand-drifts and peat-formation on the Plateau, which forced the herdsmen to move farther away from the villages (Van Gijn & Waterbolk, 1984). The suitability of the salt marshes for grazing might have resulted in 'transhumance', i.e. the movement of herds of domestic livestock to complementary seasonal pastures in the period 700–500 B.C. (Waterbolk, 1988). This system must have changed gradually into year-round occupation of the salt marshes.

The forests on elevated levees along the lower part of the rivers in the fresh water landscape were cleared very early and had completely vanished in the Roman Period in northwestern Germany. The treeless anthropogenic replacement communities *Molinio-Arrhenatheretea* grassland communities, *Chenopodietea* arable field communities and *Plantaginetea* treading communities were found from 700 B.C. onwards (Behre, 1979).

Farm-steads were built initially (ca. 600 B.C.) on the salt marsh, but later also on mounds of salt marsh sods because of transgression periods from ca. 500 B.C. onwards. These mounds gradually grew higher through the accumulation of waste and dung and, therefore, particularly through macro-fossils, became excellent records of former settlement and land use.

The dwelling places were situated at the highest points of the salt marsh viz. salt marsh ridges and creek bank levees. These were also the only places to grow arable crops (toponyme: 'valge') and were preferred as cattle-grazing areas. It has been demonstrated that crops grown from species found in the mounds can be cultivated on the upper salt marsh in the Netherlands (Van Zeist *et al.*, 1976) and in Germany (Körner-Grohne, 1967). Moreover, ploughing marks have been discovered on former salt marshes (Haarnagel, 1979). The salt marsh depressions between the creek bank levees were mainly used for hay-making (toponyme: 'meede') and sheep-grazing (Miedema, 1983).

In a salt marsh area of 150 km² northwest of the city of Groningen, the Netherlands, most mounds were only inhabited for a few centuries but the area was, as a whole, inhabited continuously from the early Iron Age (ca. 600 B.C.) onwards (Waterbolk, 1976; Miedema, 1983). Each farm-stead needed food for seven to eight people to be realised on 5 ha of arable field including the dwelling place, and 30 ha of grassland (20 cattle, 5 horses, 20 sheep/goats) (Haarnagel, 1979; Miedema, 1983). Not the whole area which was suitable for agricultural practices was indeed needed during the early Iron Age (Table 4). Only a minor part (ca. 600 ha) of the inferior lower salt marsh had to be exploited. During the late Iron Age half of the area suitable as arable land was needed and ca. 7,000 ha of the lower salt marsh was exploited as grassland. During the Roman Period all the suitable grassland was exploited and there was probably even a shortage of 700 ha which was possibly compensated for by stubble grazing of the arable fields (Miedema, 1983).

The salt marsh plant communities in the northern part of the Netherlands and adjacent Germany from the time of the mound settlements were derived from palaeo-ecological samples (see the section on original and unexploited plant communities) (Körner-Grohne, 1967; Van Zeist, 1974; Behre, 1979; 1985). The lower salt marsh contained the *Puccinellietum maritimae* and the mid salt marsh the *Juncetum gerardii*. It was assumed that only the *Juncetum gerardii leontodontetosum autumnalis* with *Lolio-Potentillion* and *Saginion maritimae* elements occurred on the upper salt marsh. It must, therefore, be assumed that the salt marshes were heavily exploited (Waterbolk, 1976), as Miedema (1983) had already suggested.

The exploitation of salt marshes continued. Hay-making has gradually decreased and nowadays the most widespread use is open-range grazing for domestic animals. Seventy% of the northwestern European salt marshes are still exploited, but the area of abandoned salt marshes increases rapidly (Bakker, 1989).

### Protection of coastal areas by dikes

The only defence against inundations were centuries long the mounds. Different settlements did not cooperate in the building of dikes as protection against the sea. A start was, most likely, made ca. 1000 A.D. in the northern Netherlands (Waterbolk, 1976). It started in adjacent Germany in the 11th century (Behre, 1985). The first low dikes enclosed cultivated salt marsh areas around one or two mounds. A closed sea-defence probably existed in Groningen and Friesland around 1100 A.D., featuring dikes with a maximum height of 2.50 m. Vast salt marsh areas, however, remained unprotected by dikes and had, therefore, no owners.

During the 12th century Cistercian monks founded the Klaarkamp Abbey near Rinsumageest in the neighbourhood of Dokkum in Friesland. They built dikes and reclaimed the unprotected salt marsh (Reitsma & Bakker, 1986).

Later on the sea reclaimed large parts of the embanked areas during flood disasters. In these flooded areas as well as in other areas outside the existing reclamations, sedimentation allowed the

*Table 4.* Area suited and needed for arable field and grassland on the salt marsh northwest of the city of Groningen during three settlement periods (after Miedema, 1983).

|  | Area suited | | Area needed | |
|---|---|---|---|---|
|  | Arable field | Grassland | Arable field | Grassland |
| Early iron age | 730 | 5400 | 160 | 1200 |
| Late iron age | 1940 | 10950 | 1000 | 6630 |
| Roman period | 1940 | 10950 | 1980 | 11660 |

growth of new foreland (for instance Middelzee, Lauwerszee, Fivel, Dollard in the Netherlands and Leybucht, Harlebucht, Jadebusen in adjacent Germany). Over the last three or four centuries, the Wadden Sea has gradually diminished in size through successive reclamation of the newly accreted salt marshes for agricultural purposes. The continuing sedimentation, however, always produced new salt marshes.

Nowadays, the growth of salt marshes is much slower and occurs in the Wadden Sea along the mainland coast under controlled conditions. The reclamation rates in the last centuries were higher than the rate of area increase of salt marsh. To compare salt marsh areas in different years and regions, the acreage of salt marsh areas are related to the extent of their tidal basins (catchment area of a tidal inlet), resulting in a proportional

share. Dijkema (1987) proposed to take the proportional share of salt marshes between 1600 and 1800 as a standard for 'naturalness' of the Dutch Wadden Sea, since a rough balance between the rate of area increase and the rate of embankment was found in that period. The mainland salt marshes of the eastern Dutch Wadden Sea area cover nowadays 50 km² less than expected from this standard (Fig. 9). This is only partly compensated for by the island salt marshes which cover 18 km² more than calculated based on the standard (the latter is due to the positive effect of sand dikes on the salt marsh growth). With unaltered area increase and without taking sea level rise into account (and no embankment) the 'naturalness' standard for the mainland salt marshes will be reached again in 70 to 135 years.
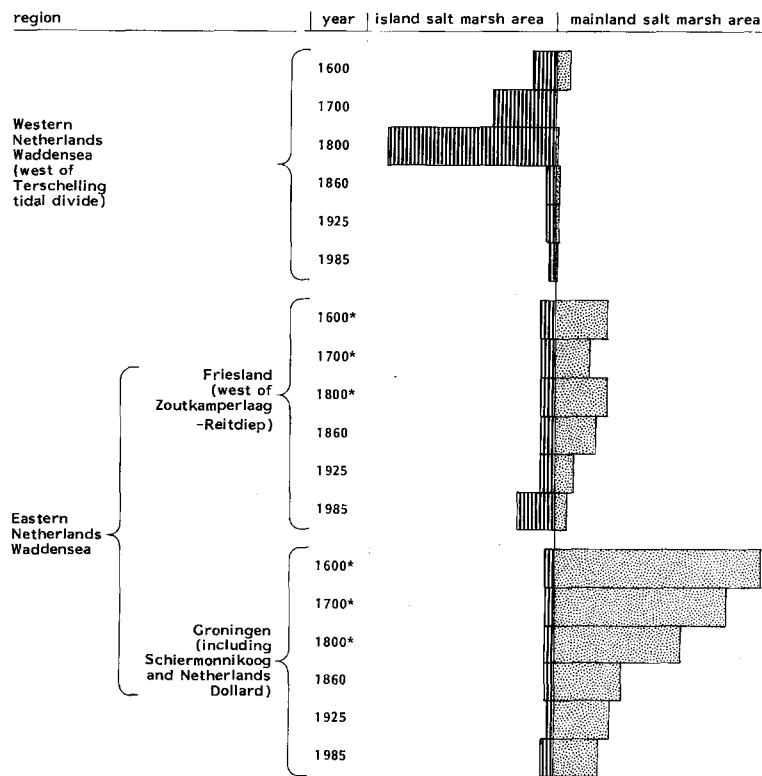


Fig. 9. Salt marsh area in the Netherlands Waddens Sea after 1600, in percentages of the total tidal area. The former island of Huisduinen has been included. Data for 1985 including the Slufter on Texel, but excluding summer polders and mainland pioneer vegetation. ------ = mean salt marsh percentage for the years 1600, 1700 and 1800 (from Dijkema, 1987, courtesy of Kluwer Academic Publishers).

## Effects of management on salt marsh plant communities

Soil aeration is a key-factor in the initial stages of salt marsh formation, namely, in the pioneer zone and low salt marsh. Soil salinity becomes more important with increasing elevation. The zonation of plant species along the gradient from tidal flats towards upper salt marsh is, however, also determined by other than abiotic factors. Competitive interactions between plant species are important in the mid- and high salt marsh in determining the zonation pattern (Snow & Vince, 1984; Bertness & Ellison, 1987). It is strongly influenced by management practices, for instance grazing and hay-making.

Cessation of grazing often caused dominance of one or a few plant species. Which species reaches dominance depends on the tidal level and salinity of the sea water, e.g. Puccinellia martitima in England (Ranwell in Beeftink, 1977b), Festuca rubra or Elymus repens in the Baltic (Schmeisky, 1977), Phragmites australis in the Baltic (Siira, 1970), Elymus pycnanthus on the barrier islands in the Netherlands (Bakker, 1989) and Germany (Andresen et al., 1990), and Atriplex prostrata and Elymus repens in mainland salt marshes of the Netherlands (Dijkema, 1983).

A successional scheme was derived from long-term studies of vegetational change after abandoning a previously grazed salt marsh, and after resumption of grazing of an abandoned salt marsh on the island of Schiermonnikoog in the Netherlands (Fig. 10). After the resumption of grazing, the return to the initial successional stage, generally took 5–10 years. After the cessation of the grazing regime it often takes 10–20 years to reach a new equilibrium (Bakker, 1989). Elymus pycnanthus outcompeted most other species. The number of plant communities as well as the number of species in each community decreased after cessation of grazing. A number of rare species, viz., Bupleurum tenuissimum, Cicendia filiformis, Cochlearia anglica, Parapholis strigosa (Wolff, 1988), are threatened in this way.

Grazing of a previously abandoned salt marsh effectuated a larger species-richness than a hay-
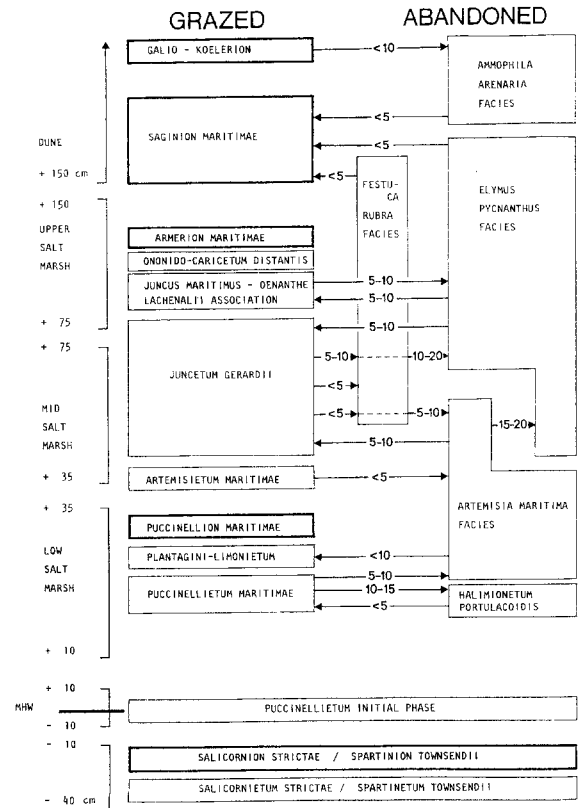


Fig. 10. The position of syntaxa with respect to MHW and the number of years it requires to change after the cessation or the resumption of heavy grazing by 1.6 heifers ha$^{-1}$ (from Bakker, 1989, courtesy of Kluwer Academic Publishers).

making regime (Bakker, 1989). This may be because grazing facilitates the establishment of more species by the creation of open spaces, while hay-making causes the formation of dense turf dominated by Festuca rubra. The species-richness on a grazed lower salt marsh is, however very low, because of the complete destruction of the topsoil by heavy grazing (Bakker, 1989).

Grazing with moderate stocking density creates a pattern of closely grazed areas and lightly grazed patches. The comparison of above-ground standing crop in the grazed and abandoned plant communities on the island salt marsh of Schiermonnikoog (Fig. 11) shows different rates of herbage utilization of the various plant communities. These differences emerged soon after the resumption of grazing, and maintained themselves. The lightly grazed patches range from one
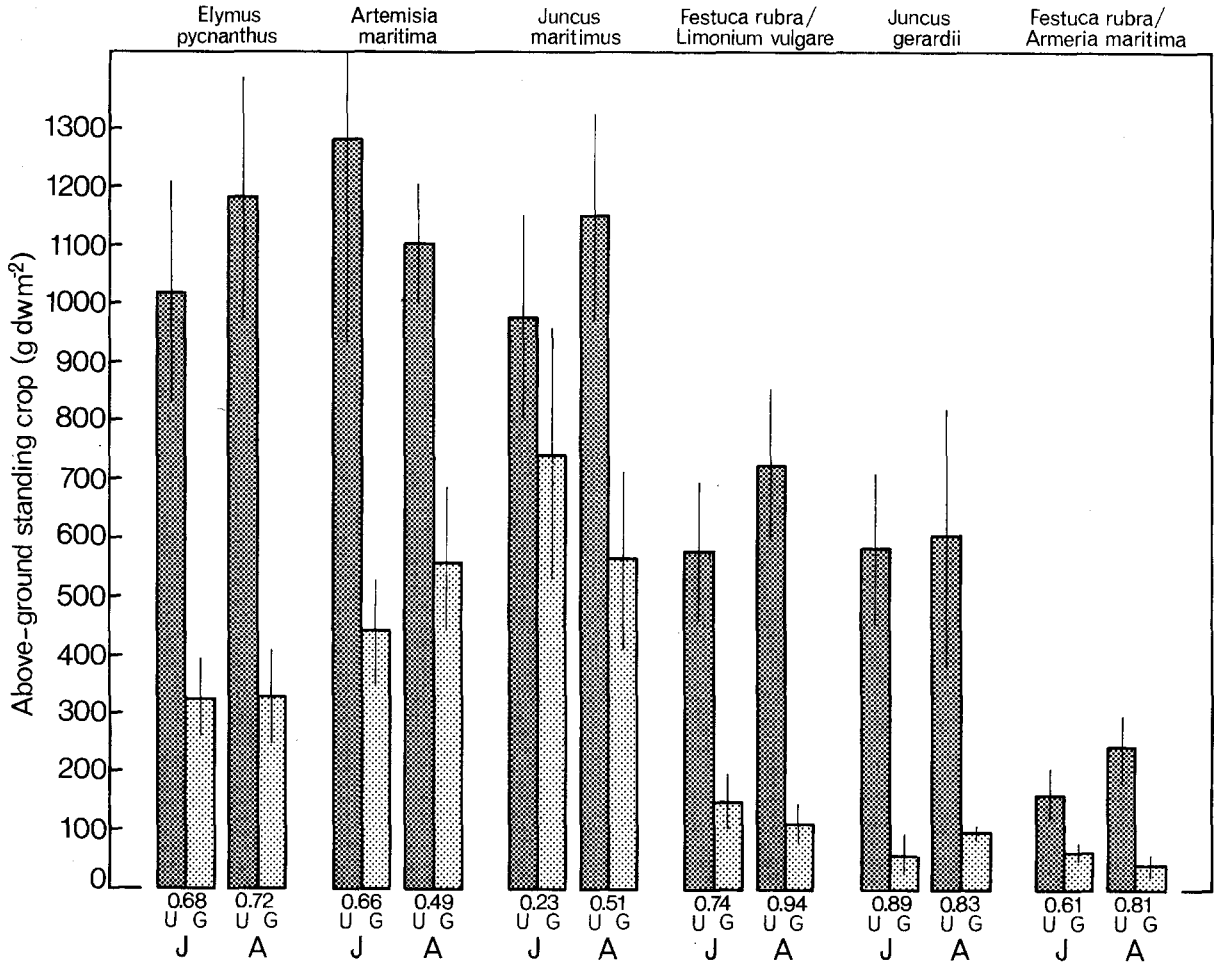
*Fig. 11.* Average above-ground standing crop including litter ( $\pm$ SE) in ungrazed (first bar) and grazed (second bar) salt marsh plant communities in June and in August. The fraction utilized, i.e. difference between grazed and ungrazed,is indicated below the bars (from Bakker, 1989, courtesy of Kluwer Academic Publishers).

ha to small isolated clumps of *Juncus maritimus* (Bakker, 1989). It was found in a mainland salt marsh that the height of the canopy increased from the dike towards the tidal flats in a grazed salt marsh. No such a trend was found in the abandoned site, which indicates a decrease of grazing impact towards the tidal flats (Andresen *et al.*, 1990).

## Effects of management on fauna

### Invertebrates

The invertebrate species diversity was highest in the *Puccinellia maritima* and the *Armerion*

*martimae* communities of the salt marshes in northern Germany (Rahmann *et al.*, 1987). The number of individuals decreased in the following sequence: abandoned for 10 years > abandoned for 1 year > cut in July > nearly 2 cattle ha$^{-1}$ > 5 sheep ha$^{-1}$. The numbers of species and faunal groups were highest in the abandoned area, with a dominance of cicades (*Cicadina*), bugs (*Heteroptera*) and snails (*Gastropoda*). The grazed areas were very poor with only beetles (*Coleoptera*) and bugs.

The effects on the macrofaunal invertebrates of cessation of cattle grazing were studied three years after the withdrawal of the grazers (Irmler & Heydemann, 1985, 1986). The number of species did

not change, but that of individuals belonging to trampling-sensitive species increased in the abandoned area, namely, springtails (*Collembola*), spiders (*Aranea*) and species feeding on tall plants or parts of them, namely, butterflies (*Lepidoptera*), aphids (*Aphinidae*), bees (*Apidae*) and hoverflies (*Syrphidae*), whereas the coprophagous species and those feeding on algae in the bare soil decreased.

The cessation of grazing caused litter accumulation and hence, the food web shifted from predominance by herbivorous animals to a food web dominated by detrivorous animals (Andresen *et al.*, 1990). On the most heavily grazed site the macrofaunal community of the lower salt marsh spread to the higher salt marsh. On the not grazed area the *Elymus pycnanthus* community had spread after eight years. Characteristic salt marsh invertebrates had disappeared within 10 years and were replaced by non-characteristic inland species (Andresen *et al.*, 1990).

*Birds*

The effect of grazing on the function of salt marshes as a foraging or resting area for birds during high tides and for breeding was studied in the German Wadden Sea area (Schultz, 1987). The increase in the number of breeding Oyster-catchers (*Haemotopus ostralegus*) was related to the increased grazing of salt marshes, whereas the number of Redshanks (*Tringa totanus*) decreased. The avifauna was in this case negatively influenced by the frequency with which the birds were disturbed by flooding, the trampling of nests and pulli, and the increased stocking density. The vegetation composition and structure was considered less important. Foraging Barnacle (*Branta leucopsis*) and Brent geese (*B. bernicla*) preferred, however, salt marshes grazed by live-stock.

**Perspectives for maintenance, management and restoration**

Best strategies for maintenance of the salt marsh ecosystem in the Wadden Sea area are being dis-

cussed for a long time (Ovesen, 1990). The management practices in Germany have focused on coastal protection and agricultural practices with hardly any attention for natural processes. Large areas of salt marshes are designed nature reserve recently, and the major part is abandoned now. This is in contrast to the Dutch and Danish management, where extensive grazing is the predominant management regime.

Coastal protection in Germany included until recently facilitation of a maximal sedimentation in man-made salt marshes. The marsh was considered to be heavily drained and grazed since ungrazed salt marshes were perceived to erode more easily. An opposite management was chosen by nature conservation authorities, namely abandonment, which resulted in a decrease in plant and animal species-richness.

The Duch salt marshes are nowadays marginal agricultural areas and it is, therefore, difficult to have them grazed by domestic live-stock. One of the private organizations for nature conservation in the Netherlands brings Limousin cattle to the salt marsh for the summer period, whereas the cattle are brought to the Drenthe Plateau for the winter period and then forage on hay cut from inland nature reserves. It seems to be the beginning of a modern 'transhumance'.

The second trilateral working conference on salt marsh management in the international Wadden Sea area held in October 1989 at Rømø, Denmark, agreed on a number of recommendations (Ovesen, 1990), of which some important ones are listed below:

1. Land reclamation activities should not be carried out in areas where natural sedimentation is taking place considering the fact that erosion and sedimentation are natural processes. The potential expansion of salt marsh areas, by the local removal of summer dikes, should be considered.
2. Protection measures for existing salt marshes should be applied in a differentiated and specific manner. Attention should be paid, in particular to the pioneer zone of the mainland salt marshes to prevent cliff formation becoming a

widespread process. The grazing of salt marshes for coastal protection is unnecessary.

3. Drainage should be based on natural processes and not on man-made technical means.

4. Vegetation management by grazing is to be preferred and should be performed on large areas of 100 ha or more to produce a mosaic of different vegetation types. An advocated maximum stocking density is one head of cattle $ha^{-1}$ or two sheep with their lambs, grazing by horses should be avoided due to turf destruction and associated erosion risk.

5. The vegetation pattern should include areas with short vegetation cover (grazed) and areas with long vegetation cover (ungrazed or very lightly grazed). The determination of the ratio of grazed and ungrazed areas should be based on the results of grazing experiments.

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