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Does zonation reflect the succession of salt-marsh vegetation? A comparison of an estuarine and a coastal bar island marsh in The Netherlands

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SUMMARY

Traditionally, vegetation succession in salt-marshes has been inferred from the zonation of the vegetation. However, long-term observation of species composition in salt-marshes has led to the recognition that the change of the vegetation does not always proceed according to the succession schemes derived from zonation. The hypothesis that the zonation of the vegetation reflects its succession is based on a model which assumes that the relief in the marsh is formed by sediment trapped by the vegetation. According to this model the present high marsh developed from a low marsh and the low marsh of today will rise to higher levels.

In this study we investigated the sedimentary record in a coastal bar island marsh and in an estuarine salt marsh, in order to detect whether the formation of the relief in these two marshes corresponds to this geomorphogenetic model. The sedimentary record in the estuarine marsh supports the hypothesis that the relief was formed by sediments deposited in a marsh environment. The formation of the relief in the marsh at the coastal bar island, however, could not be attributed to marsh sediments solely. The surface relief is mainly determined by the relief of the sandy subsoil. Historical evidence indicates that the relief of the sandy subsoil had been formed by aeolic processes in a beach environment one century ago, and has subsequently been fossilized.

The vegetation displayed a marked zonation in both marshes. The present zonation would suggest that succession in the estuarine marsh was initiated by *Spartina anglica*§, which was confirmed by 50-year-old aerial photography. It was concluded that historic succession could be inferred from zonation in the estuarine marsh, but not in the marsh at the coastal bar island.

Key-words: accretion, geomorphogenesis, salt-marsh vegetation, succession, zonation.

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§Nomenclature of the species follows Tutin *et al.* (1964–80).

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INTRODUCTION

Zonation is a general feature of salt-marsh vegetation (Chapman 1974; Long & Mason 1983; Adam 1990). It has been suggested that this zonation reflects the succession of the vegetation (Clements 1916; Chapman 1974; 1977). This hypothesis provided the basis for the numerous succession schemes for salt-marsh vegetation (Chapman 1974). More recently, models inferred from zonation have been applied to predict the response of salt-marsh vegetation to a change of the tidal regime (De Jong & De Kogel 1985; De Leeuw *et al.* 1993).

However, results of long-term monitoring reveal that the dynamics of salt-marsh vegetation does not always proceed according to the succession schemes inferred from zonation. The response of salt-marsh vegetation to a 26 cm tidal reduction caused by the construction of the Oosterschelde storm surge barrier was correctly predicted by a model inferred from zonation (De Leeuw *et al.* 1993). Scott Warren & Niering (1993) described changes in salt-marsh vegetation which were attributed to a gradual drowning of the marsh. Adam (1990) remarked that rapid succession of salt-marsh vegetation has been recorded in some cases, but in most studies community boundaries remained relatively stable for decades. Roozen & Westhoff (1985) monitoring permanent plots for 30 years observed considerable change of the vegetation, which could not, however, be interpreted as a change towards a species composition characteristic of a different zone.

The hypothesis that zonation reflects succession is based on the assumption that the relief in the marsh determining the zonation was formed by sediments trapped by the vegetation. According to this hypothesis low marsh species colonizing bare tidal flats stabilize the substrate. The presence of plants promotes accretion, thus raising the surface. This would allow other species to invade the marsh, and eventually the early colonizers will be lost. This process would continue until the marsh is raised above the height of the highest tides (Steers 1977). Hence, a detailed knowledge of the geomorphogenesis of the marsh under study would be required in order to decide whether succession may be inferred from the zonation of the vegetation. Surprisingly enough, however, in succession studies little attention has been addressed to the question whether the formation of the marsh corresponds to this geomorphogenetic model.

In this study we investigate whether succession may be inferred from zonation by comparing the sedimentary record and the distribution of species along the marsh elevation gradient in two contrasting salt-marshes in The Netherlands: an estuarine marsh in the south-west and a marsh situated at a coastal bar island in the North.

MATERIAL AND METHODS

Description of the study area

The sedimentary record and the vegetation was investigated in two marshes in The Netherlands. The Zuidgors is a marsh of the estuarine type (Beeftink 1977) situated near the village of Ellewoutsdijk along the Westerschelde estuary in the SW Netherlands (Fig. 1). Beeftink (1965) described the vegetation of the estuarine salt-marshes in the SW Netherlands and presented succession schemes inferred from zonation. The Oosterkwelder is a marsh of the Wadden type (Beeftink 1977) situated on the coastal bar island of Schiermonnikoog in the north of The Netherlands (Fig. 1). Westhoff (1947) described the salt-marsh vegetation of the Wadden Islands in the north of The Netherlands and

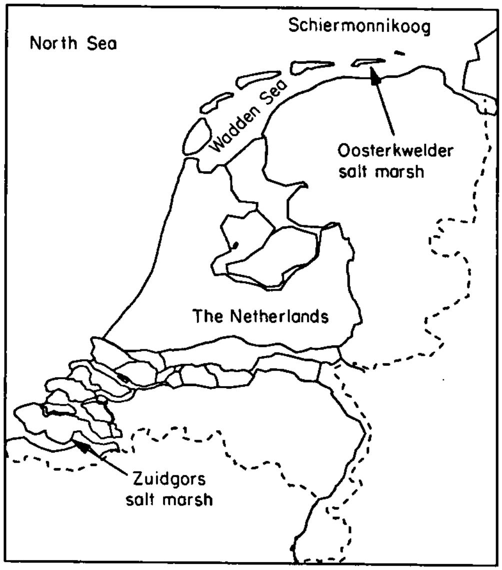

Fig. 1. Map of The Netherlands indicating the Zuidgors marsh situated along the Westerschelde estuary and the Oosterkwelder marsh located on the coastal bar island of Schiermonnikoog.

suggested that the different plant communities formed a halosere (a successional sequence).

Vegetation and soil analysis

In order to describe the spatial changes of soil and vegetation along the elevation gradient we established transects perpendicular to the main relief in both marshes. In the Zuidgors marsh, 672 1-m^2 plots were sampled along a line transect of 450 m (Fig. 2). In the Oosterkwelder, 551 1-m^2 plots were sampled in a transect 50 m long and 10 m wide.

In the classical model of marsh formation it is assumed that the marsh level rises through accretion. Hence, we investigated the relation between the relief of the surface and the thickness of the clay horizon. For every plot we measured elevation (cm) with respect to Dutch Ordnance Level (NAP) using a theodolite. A soil auger was used to determine the thickness of the clay horizon underlying the soil surface. The thickness of the clay horizon was estimated from the depth at which we observed a change from finer sediments to a firm and continuous layer of sand. Generally, this was an abrupt transition which could easily be detected visually. In the estuarine marsh there was sometimes a more gradual transition, the bands of clay alternating with smaller bands of sand. In these cases we continued augering until a continuous layer of sand was observed, and considered this depth to represent the thickness of the clay horizon.

The presence of species in the 1-m^2 plots was recorded. We used the CURVE (Huisman *et al.* 1993) module of VEGROW (Fresco 1990) to fit five regression models describing the probability of occurrence of species along the marsh elevation gradient. The curves were fitted according to

$$y = \frac{1}{1 + e^{a + bx}} * \frac{1}{1 + e^{c + dx}}$$

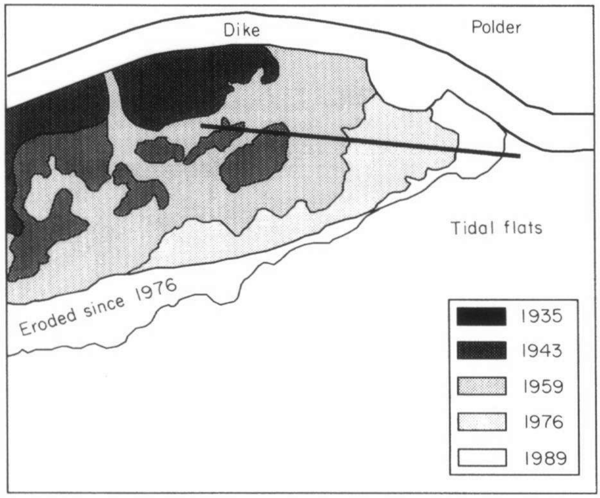

Fig. 2. Map of the estuarine Zuidgors marsh showing the transect sampled (solid line) and the area of the marsh vegetated by marsh macrophytes, as inferred from aerial photography, in 1937, 1943, 1959, 1976 and 1989.

where y and x are the response and the explanatory variable respectively and a, b, c and d the parameters to be estimated. The equation can describe a straight line, a one-sided sigmoidal curve increasing to a probability of one, a one-sided sigmoidal curve increasing to a probability lower than one, a symmetric distribution and a skewed distribution.

Marsh history

Aerial photographs taken in 1935, 1943, 1959, 1976 and 1989 were used to study the development of the estuarine Zuidgors marsh. First, we studied the horizontal extension of the marsh edge. Secondly, we investigated whether *Spartina* was involved in the colonization of the marsh. *Spartina anglica* was introduced in the Westerschelde estuary in 1925 (Jansen & Sloff 1938). When colonizing tidal flats *Spartina anglica* forms clones which appear on aerial photographs as distinct circular features. We investigated the aerial photographs for these features.

Topographic maps were used to reconstruct the history of the island of Schiermonnikoog. The following maps were used: the 1:115 200 Krayenhof map of 1820, the 1:50 000 topographic map of 1860 (survey executed in 1854), the 1:50 000 topographic map of 1930 (survey in 1927) and the 1:50 000 topographic map published in 1971 (survey in 1969).

RESULTS

History of the estuarine marsh

Aerial photography revealed that the estuarine marsh has been expanding in an eastward direction since 1935 (Fig. 2). The western more inland part of the transect was colonized by marsh vegetation in the 1940s and 1950s. We will refer to this part of the transect as the old marsh. The middle end of the transect has become vegetated after 1960. We will refer to it as the young marsh.

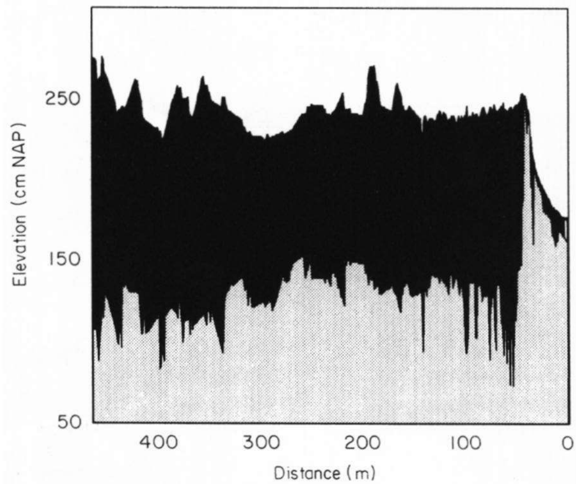

Fig. 3. Transect showing the elevation of the marsh surface in relation to the thickness of the clay horizon (black) overlaying the sandy subsoil (shaded) in the estuarine Zuidgors marsh.

No photo characteristics indicating the presence of *Spartina anglica* could be detected on the 1935 photographs. However, dark-toned circular features characteristic of *Spartina anglica* were observed on the tidal flats on the 1943 photographs. Parts of the tidal flats, which were devoid of vegetation in 1935, were also covered by continuous vegetation in 1943. These areas have a grey tone corresponding to the *Spartina anglica* patches, while the grey tone differed from the older parts of the marsh. This indicates that *Spartina anglica* had colonized the tidal flats between 1935 and 1943. The same circular features could be detected on aerial photography in later years. However, by this time the areal extent of this *Spartina anglica* zone was much smaller than on the 1943 photographs.

History of the island marsh

Analysis of historic maps and aerial photography revealed that the transect in the marsh at the coastal bar island has at least been vegetated since 1927. On the maps published in 1820 and in 1860 the area is indicated as a beach. Survey for the later maps was carried out in 1854. The same area is represented as a marsh on the 1:50 000 topographic map published in 1930. Field work for this map was carried out in 1927. Together, the data indicate that the area changed from a beach into a marsh somewhere between 1854 and 1927. Hence, it is concluded that the marsh is aged somewhere between 65 and 140 years.

The Kooiduinen formed the eastward dune system in 1820 (Fig. 4). A new dune system running from south-west to north-east is represented on the 1860 map. Little of this dune system remained by 1930. Instead, on the 1930 map a new dune system, running nearly perpendicular to the old system from north-west to south-east, is presented. It is therefore concluded that the older dune system had been eroding between 1854 and 1927 while the new dune system was formed in the same period.

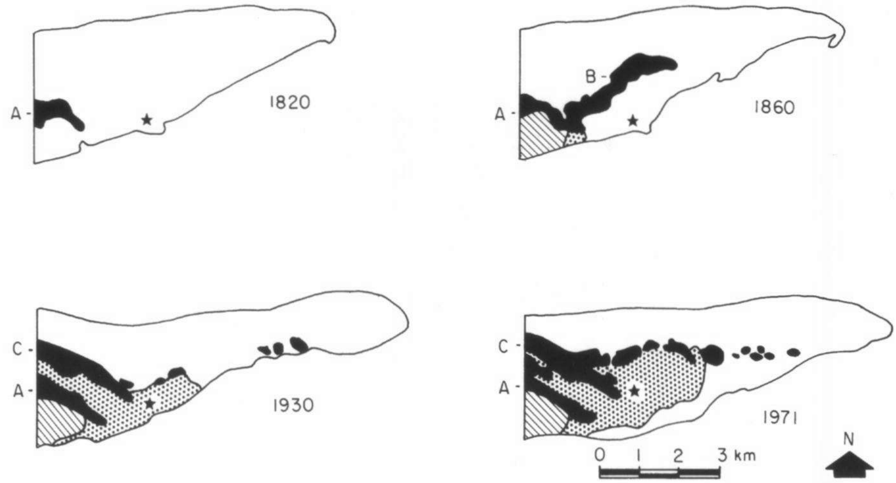

Fig. 4. Map of the island of Schiermonnikoog showing the location of the transect (asterisk), and the area covered by beaches (white), dunes (black), salt-marsh (shaded) and polder (hatched) according to the maps of 1820, 1860, 1930 and 1971. The major dune systems have been indicated as follows: A, Kooiduinen; B, the dune system on the 1860 map later eroded away; C, the Kobbeduinen dune system.

Geomorphology of the estuarine marsh

The transect in the estuarine marsh runs from east to west (Fig. 2). The marsh surface is highest in the west and gradually decreases towards the east (Fig. 3). The transect crosses several depressions intersected by creeks. These creeks are adjoined by creek banks which rise 10–20 cm above the general terrain level. At the eastern end the transect enters the adjoining tidal flats. The upper parts of the tidal flats forms the lower end of the transect in the estuarine marsh (Fig. 3). This part of the transect is formed by sloping sandy sediments which have been covered by a shallow layer of clay. The slope of the surface gradually rises from 1% on the tidal flat to 5% near the cliff which adjoins the marsh (Fig. 3).

Shallow layers of clay were observed on top of the sandy substrate in the tidal flats. To the west behind the cliff which forms the transition to the marsh, the thickness of the clay horizon increases to approximately 1 m in the young part of the marsh. Further to the west in the old marsh, the clay horizon is 1·5 m or more thick.

Geomorphology of the island marsh

The transect in the marsh at the coastal bar island runs from a higher sloping area into the centre of a depression (Fig. 5). The highest sloping part of the transect forms the foot of a small dune. The soil is sandy throughout, without clay on top. The thickness of the clay layer increases down the slope to approximately 10 cm in the depression. Therefore, the relief in the marsh cannot be attributed to the accumulation of sediments deposited in a marsh environment. Instead, the relief of the marsh surface strongly reflects the relief of the underlying sandy substrate (Fig. 5). The relief of this sandy substrate most likely dates from the time before the colonization by marsh macrophytes.

Species distribution in the estuarine marsh

Ten species were observed in the samples from the estuarine marsh. Most species are restricted to a particular zone of the marsh (Fig. 6). *Spartina anglica* and *Salicornia*

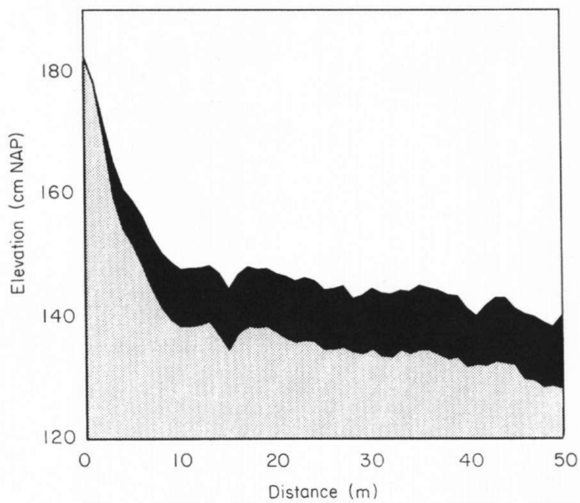

Fig. 5. Schematic cross-section of the transect sampled showing the elevation of the marsh surface and the thickness of the clay horizon (black) overlaying the sandy subsoil (shaded) in the Oosterkwelder marsh at the island of Schiermonnikoog.

europaea show an optimum at the low end of the gradient. *Puccinellia maritima, Aster tripolium, Suaeda maritima* and *Halimione portulacoides* show an optimum at intermediate levels. *Elymus pycnanthus* and *Atriplex prostrata* are confined to the highest parts of the marsh.

Species distribution in the island marsh

Seventeen species were recorded in the 551 samples from the marsh at the island of Schiermonnikoog (Fig. 7). Three species, *Juncus gerardi, Atriplex prostrata* and *Artemisia maritima*, occur along the whole gradient. One species, *Elymus*, is present in all the higher samples. *Juncus maritimus* shows an optimum at intermediate elevations. Four other species, *Glaux maritima, Plantago maritima, Spergularia media* and *Limonium vulgare*, display an optimum near the lower end of the gradient. The optimum of eight other species, including *Puccinellia, Salicornia, Halimione* and *Aster*, is out of the range of the gradient sampled.

DISCUSSION

In this study we described the distribution of species and the sedimentary record in two marshes in The Netherlands, in order to investigate whether succession of salt-marsh vegetation may be inferred from zonation. First, we investigated whether the relief of the marsh could be attributed to accretion of marsh sediments. A positive relation exists between thickness of the clay horizon and marsh level in the estuarine marsh. This implies that the higher parts of the transect, which happened to be older, are higher because more sediment had been deposited. We therefore conclude that the relief in the estuarine marsh has been formed through accumulation of sediments in a marsh environment.

The relief in the island marsh is not positively related to the thickness of the clay horizon. Instead, the thickness of this horizon decreases with increasing elevation. The

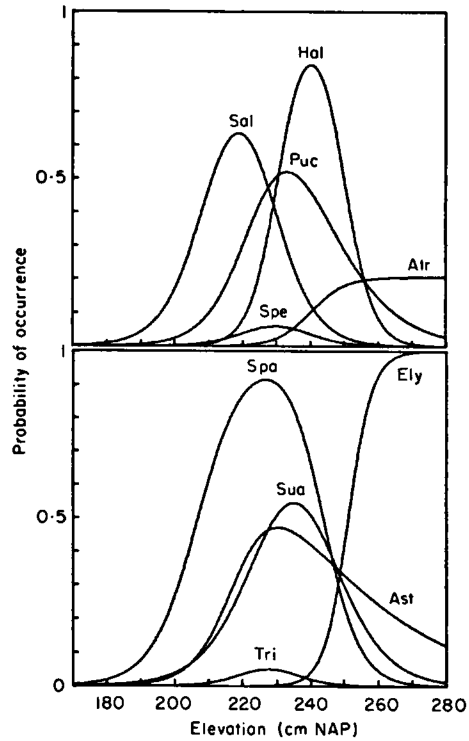

Fig. 6. Probability of occurrence of species along the marsh elevation gradient in the estuarine Zuidgors marsh. Sal, *Salicornia europaea*; Spe, *Spergularia media*; Puc, *Puccinellia maritima*; Hal, *Halimione portulacoides*; Atr, *Atriplex prostrata*; Spa, *Spartina anglica*; Sua, *Suaeda maritima*; Tri, *Triglochin maritima*; Ast, *Aster tripolium*; Ely, *Elymus pycnanthus*.

relief of the marsh surface in the island marsh strongly reflects the relief of the underlying sandy substrate. Comparison of old maps revealed that the marsh has been vegetated for at least 65 years. As uninterrupted layers of sand are not deposited in a salt-marsh environment, this implies that the relief in the sandy substrate was formed under different environmental conditions more than 65 years ago.

Analysis of historical maps revealed that the location of the transect in the island marsh formed a beach in the beginning of the nineteenth century. A dune system which traversed this beach in the middle of the nineteenth century had been eroded away in the early twentieth century (Reitsma & Bakker 1986). Meanwhile a new dune system, oriented perpendicular to the old one, had been formed.

This indicates that the area in which our transect was located has been a highly dynamic environment during the second half of the nineteenth century. The type of relief observed in the sandy substrate is typical for dynamic beach environments. Hence, this suggests that the relief of the sandy substrate in the transect was formed in a beach environment more than 65 years ago. Most of the present relief still reflects this older fossilized beach landscape. Only part of the relief of today, the thin layer of clay, has been formed in a salt-marsh environment.

Next the distribution of species along the vertical gradient was investigated. The vegetation displays a marked zonation in both marshes. There exists, however, a difference in species composition along the two gradients. *Spartina anglica*, the most

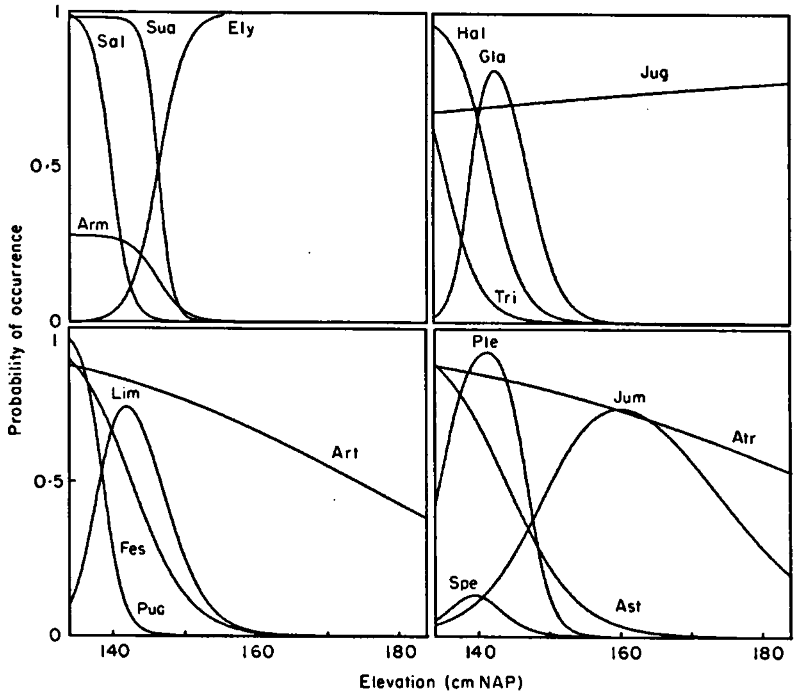

Fig. 7. Probability of occurrence of species along the marsh elevation gradient in the island marsh. Sal, *Salicornia europaea*; Arm, *Armeria maritima*; Sua, *Suaeda maritima*; Ely, *Elymus pycnanthus*; Hal, *Halimione portulacoides*; Tri, *Triglochin maritima*; Gla, *Glaux maritima*; Jug, *Juncus gerardi*; Puc, *Puccinellia maritima*; Fes, *Festuca rubra*; Lim, *Limonium vulgare*; Art, *Artemisia maritima*; Pla, *Plantago maritima*; Spe, *Spergularia media*; Jum, *Juncus maritimus*; Atr, *Atriplex prostrata*; Ast, *Aster tripolium*.

frequent species in the lower part of the gradient in the estuarine marsh, is not observed in the transect at the island of Schiermonnikoog. *Puccinellia maritima* occurs with a higher frequency in the lower part of the gradient in the coastal bar marsh than in the estuarine marsh. This agrees with Scholten & Rozema (1990), who found that *Puccinellia maritima* predominated in the sandy Wadden marshes while *Spartina anglica* was dominant in the clayish estuarine marshes in the SW Netherlands. Species like *Juncus gerardi* and *Festuca rubra* also occur with high frequency on the island marsh but not in the estuarine marsh. When classifying the vegetation of British salt-marshes, Adam (1978) recognized three types of salt-marshes, two of which correspond to the marshes described in this study: the Schiermonnikoog marsh corresponds to Adam's type A marsh, while the estuarine marsh along the Westerschelde corresponds to the type B marshes. In the UK, type A marshes generally prevail on sandier substrate, while the type B marshes occur on heavier soils (Adam 1978). Grazing has been suggested as an alternative cause for the differences between the marsh types (Adam 1978). Of the transects described in this study, only the one in the island marsh is grazed for a short period in spring by migrating geese (H. Olff, unpublished data).

It was argued above that the formation of the estuarine marsh corresponds to the geomorphogenetic model that forms a basic assumption of the classical succession theory, while in the coastal bar marsh it does not. Because the relief of the Oosterkwelder marsh has not been formed in a marsh environment, it follows that the part of the transect presently covered by high-marsh vegetation has never been vegetated by the species which now occur lower down the gradient. Hence, the present zonation does not reflect the historical succession of the vegetation.

The condition of *in situ* formation of the relief was fulfilled in the estuarine marsh. However, even then zonation may not reflect past succession. The succession scheme inferred from zonation in the Zuidgors marsh suggested that the marsh was colonized by *Spartina anglica.* As Adam (1990) remarked, one has to be cautious to infer succession from zonation when *Spartina anglica* is involved. *Spartina anglica* had been introduced in the Westerschelde estuary in 1925 (Jansen & Sloff 1938; Beeftink 1965). Jansen & Sloff (1938) reported that the species was present in the estuarine Zuidgors marsh in 1937. Furthermore, the aerial photographs demonstrated that the oldest parts of the transect have been colonized between 1935 and 1943, and that large parts of the tidal flats have been colonized by *Spartina anglica* between 1935 and 1943. This indicates that *Spartina anglica* has been involved in the early colonization of the oldest parts of the transect sampled. It is therefore concluded that the present zonation may reflect succession in the estuarine marsh over the past 57 years.

Together, these results indicate that the historical succession may be inferred from zonation in the estuarine marsh but not in the island marsh. This difference has been attributed to the geomorphogenesis of the two marshes investigated. The differences in geomorphogenesis depend largely on the landscape setting within which these two marsh systems were formed. On coastal bar islands aeolic processes form a relief on the beaches before these environments are colonized by marsh macrophytes. The relief on estuarine tidal flats is scarcely or not at all affected by such aeolic processes. Aeolic processes are more important on coastal bar islands because they are more exposed to the action of the wind. As compared to coastal lagoons, the higher sediment load of estuarine waters might determine the higher accretion rates in the estuarine marshes.

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