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Reconstruction of an interrupted primary beach plain succession using a Geographical Information System

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Abstract. This study reports on a primary succession on a beach plain on the Dutch Wadden island of Schiermonnikoog. Vegetation succession started in 1959 when a sand dike was constructed to prevent structural erosion of the area by storm floods. Since then the sandy beach behind the dike has been protected from the direct influence of the North Sea. Heavy storms in 1972, however, created a large gap in the dike which has remained open since. Occasional storm floods during winter penetrate deeply into the area and salt water can cover parts of the beach plain for several months. This had a pronounced impact on the vegetation. Vegetation maps for six different years and data from a permanent plot have been used to reconstruct vegetation succession over a 42-yr period. Certain parts of the area seem to have changed little, while others have developed a grassland or scrub cover. The heavy storms and associated processes such as sand blowing, intensive flooding and increased salinity have created a disturbance/stress gradient of progressive and regressive succession across the beach plain. In certain places the vegetation cover has repeatedly been destroyed and succession re-initiated. It is concluded that the different stages of succession and associated diversity of plant species only can persist through the maintenance of the natural dynamics of the area.

Keywords: Conservation; Disturbance; Inundation; Natural dynamics; Salinity.

Nomenclature: Names of vascular plants according to van der Meijden et al. (1990).

Introduction

Measures to stabilize sand movement and afforestation in sand dune environments have caused a pronounced decline in biodiversity in many areas along the European coast (Westhoff 1989; van Dijk & Grootjans 1993). This has led to ongoing succession in the dune area where shrubs and tall grasses have taken over at the expense of competitively inferior rare plant species. This process has been accelerated by the atmospheric deposition of nitrogen from industrial and agricultural areas (ten Harkel & van der Meulen 1995) and by the decline in the number of rabbits as a result of the disease myxomatosis (Ranwell 1960; Dobson & Crawley 1994). Therefore management practices such as mowing, grazing or soil cutting, are necessary to stop or retard the decline of many endangered plant species.

The present study focuses on a coastal defence project which started in the late 1950s. It has had unforeseen but beneficial results for nature conservation as a result of its failure!

Primary succession on beach plains normally starts on bare sediments. Without disturbance, the slow accumulation of nutrients over time results in increased plant biomass, which in turn captures a larger proportion of the incident light. Disturbance is here defined as "any relatively discrete event in time that disrupts an ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment" (Petraitis et al. 1989). Disturbance can influence succession in a distinct way. It may reduce the intensity of competition by removing competitors and by increasing resource availability (Wilson & Tilman 1993), or it may set back succession depending on the intensity and frequency of disturbance (Connell & Slatyer 1977).

The present study deals with some aspects of a primary succession in a coastal beach plain where disturbance by major flood events has created a mixture of different successional stages. We present an approach to reconstruct vegetation development in the area over a 42-yr period using aerial photographs and vegetation maps obtained at several intervals in combination with annual surveys of vegetation composition over a 17-yr period along a permanent transect in a relatively undisturbed part of the site (Olff et al. 1993; van Tooren et al. 1983).

Study area

The study area is located on the Wadden island of Schiermonnikoog, The Netherlands, at 53° 29 'N, 6° 12 'E (Fig. 1). Until the late 1950s, the area was an almost bare sand flat with scattered young dunes up to 2 m high. The dunes were sparsely vegetated with grasses such as *Elymus farctus* and *Ammophila arenaria*. The low-lying areas

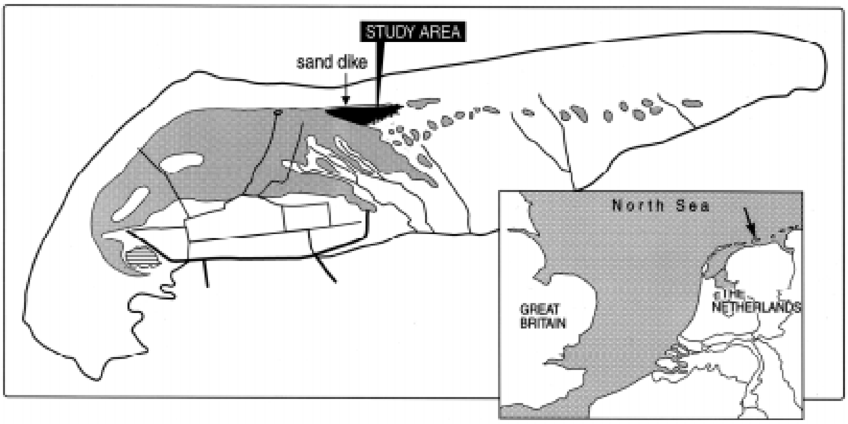

Fig. 1. The Wadden island of Schiermonnikoog with the study area and the position of the sand dike indicated.

were bare or sparsely covered with pioneer species such as *Salicornia europaea, Suaeda maritima* and *Glaux maritima*. After the construction of a ca. 5 m high sand dike in 1959, the area was protected from the direct influence of the North Sea, and plant colonization started. Heavy winter storms, however, soon created large gaps in the dike all of which were closed by the coastal defence authorities until 1972. Since then a large gap has remained open and the maintenance of the dike to the east of this gap has ceased. Storm floods from the North Sea side occur on an irregular basis (0 to 15 times per winter; Schat 1982) and sea-water can also penetrate the beach plain from the adjacent salt marsh via tidal creeks connected to the Wadden Sea (van Tooren et al. 1983). This sea water may stay in the beach plain for months. Near the large gap in the dike sand blowing occurs, sometimes covering large parts of the surrounding vegetation.

The water table in the lower parts of the beach plain usually drops below the soil surface by April or May. In September the water table is ca. 30 - 50 cm below the soil surface, although depths of 1 m may be reached in very dry summers (Olff et al. 1993). Since the capillary rise of the soil water exceeds 1 m (Rozema 1978) the sediment of the lower parts always remains moist. The salinity in the sediment may fluctuate considerably due to variations in flooding frequency and precipitation surplus (van Tooren et al. 1983). These fluctuations in salinity do not occur on the dry dunes, but the dune slopes form an unstable transitional zone between these extremes. The most western part of the plain is influenced by fresh groundwater which discharges from the adjacent dune areas (Beukeboom 1976).

The research site is designated as a nature reserve where a less strict policy with regard to maintenance of the coastal defence function will be applied (Hillen & Roelse 1995).

Methods

Vegetation maps from six different years were used to reconstruct vegetation development in the beach plain during the last 42 yr. The maps cover almost the entire beach plain of ca. 155 ha. Initially, a vegetation map was made in 1978 based on aerial photographs at a scale of 1 : 5000 and 163 stratified-randomly located vegetation samples (Wapenaar 1980). 28 vegetation types were recognized. Aerial photographs and 57 vegetation samples from earlier surveys were used to reconstruct vegetation maps for 1952, 1959, 1970 and 1976 (van der Laan 1980) at a scale of 1 : 5000. In 1994 a new vegetation map at a scale of 1 : 2000 was made based on aerial photographs and vegetation relevés. 30 local vegetation types were distinguisted which matched the previous vegetation surveys.

Spatial comparison of the different vegetation maps was performed using the Geographic Information System, ILWIS (The Integrated Land and Water Information System; Valenzuela 1988). Each digitized map consisted of 62 063 pixels, each pixel approximating to an area of $5\ m \times 5\ m$ in the field. This equalled the resolution of the earlier vegetation maps.

The different sets of vegetation units were categorized in relation to the different stages of succession for both the lower areas of the plain and the dry dunes. This classification was possible because we had detailed information on the actual succession in a relatively undisturbed part of the beach plain over a 17-yr period (1972 to 1989). The information was obtained from a grid situated in the western part of the beach plain, consisting of 12 permanent transects each 20 m long and separated by a distance of 1 m. The presence of every species was recorded each year in August in adjacent $1\ m \times 0.4\ m$ plots along the 12 transects . The transects included a low lying sand flat, a dune slope and a

Table 1. The most dominant species (bold) and some of the co-occurring species of different vegetation types grouped and sorted into distinct successional stage categories for both beach plain and dune habitats in a beach plain succession on the Wadden island of Schiermonnikoog. The plain succession can be divided into a main part, where salinity and flooding are prevalent, and a minor part in the west where, due to a higher altitude and upwelling of freshwater, a more brackish vegetation can develop.

Category	Beach plain	Dune
1	Water	
2	< 25 % cover; ***Glaux maritima***, ***Salicornia europaea***, *Suaeda maritima*	***Elymus farctus***, ***Ammophila arenaria*** *Sonchus arvensis, Festuca rubra*
3	>50% cover; ***Glaux maritima***, ***Suaeda maritima***, *Agrostis stolonifera, Puccinellia distans*	***Ammophila arenaria***, ***Hippophae rhamnoides*** *Festuca rubra, Sonchus arvensis*
4	***Festuca rubra***, ***Juncus gerardi***, *Agrostis stolonifera, Odontites vernus, Salix repens, Elymus athericus, Centaurium littorale, Linum catharticum*	***Festuca rubra, Agrostis stolonifera***, *Calamagrostis epigejos, Elymus farctus, Leontodon saxatilis, Hippophae rhamnoides, Linum catharticum, Trifolium repens*
5	***Juncus gerardi, Juncus maritimus, Festuca rubra*** *Odontites vernus, Agrostis stolonifera;* western part: ***Schoenus nigricans***, *Salix repens, Phragmites australis*	***Hippophae rhamnoides,*** *Elymus athericus, Elymus farctus, Chamerion angustifolium, Phragmites australis*
6	***Scirpus maritimus***, ***Juncus gerardi, Agrostis stolonifera*** *Juncus maritimus, Phragmites australis;* western part: ***Schoenus nigricans***, *Parnassia palustris, Salix repens*	***Hippophae rhamnoides, Salix repens,*** *Chamerion angustifolium, Calamagrostis epigejos, Urtica dioica, Senecio jacobaea*
7	***Scirpus maritimus, Phragmites australis,*** *Juncus maritimus, Juncus gerardi, Agrostis stolonifera*	***Hippophae rhamnoides, Calamagrostis epigejos, Salix repens,*** *Sambucus nigra, Calamagrostis epigejos, Urtica dioica, Holcus lanatus*
8	***Phragmites australis,*** *Scirpus maritimus;* western part: ***Schoenus nigricans***, *Parnassia palustris, Salix repens, Epipactis palustris, Liparis loeselii*	***Hippophae rhamnoides, Sambucus nigra***, *Calamagrostis epigejos*
9	western part: ***Salix pentandra, Betula pendula***	***Sambucus nigra,*** *Hippophae rhamnoides, Chamerion angustifolium, Urtica dioica, Holcus lanatus*

dry dune (further details in van Tooren et al. 1983). These data were used to estimate the change in probability of occurrence of a species during succession for the three different topographic positions. The results were then used to calculate, for each vegetation unit, the percentage similarity with the vegetation recorded in the permanent transects for each year and topographic position (further details in Olff et al. 1993). In this way each vegetation type on every map was labelled with a successional age and a topographic position. Vegetation types of the unstable transitional slope were divided, according to their similarity to either plain or dune vegetation type. Vegetation types which fell outside the time range of the permanent transect were identified using the presence of either pioneer species and bare soil or late successional species such as trees and shrubs.

The different sets of vegetation types, divided in plain and dune vegetation and labelled with their successional age, were grouped and sorted in distinct categories ranging from 1 to 9, reflecting different stages of succession along the chronosequence. New maps, representative of the different years, were made based on these different categories of succession. The areas occupied by these categories were computed as a percentage of the total area.

Finally, in order to summarize and quantify the progress of succession in the different parts of the beach plain, the variance of the category numbers of succession of the six maps was calculated for each pixel. Because in 1952 almost the whole site consisted of bare soil nearly every pixel starts with the lowest successional category. Therefore, a low variance indicates a minor vegetation change and a high variance indicates a major vegetation change (for an example see Table 2).

Results

Description and categorization of the vegetation maps

The different vegetation types are grouped in nine distinct categories of stages of succession for the two topographic positions: plain and dune (Table 1). The plain sequence starts with water or bare soil with less than 25 % vegetation cover and ends with dense vegetation of tall marsh species such as *Phragmites australis* or *Scirpus maritimus*. The succession in the westernmost part of the beach plain differs from the main part and this

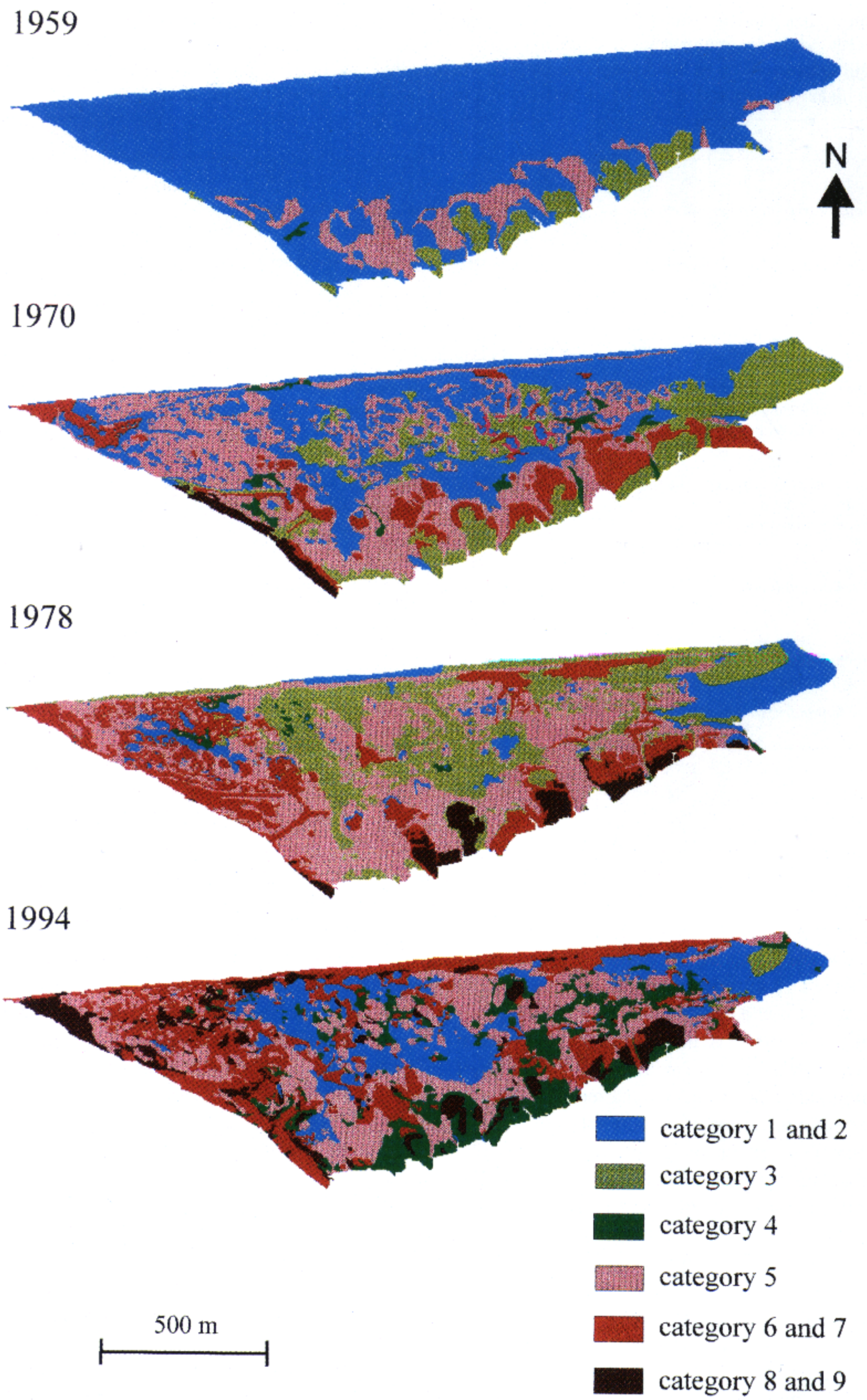

Fig. 2. Maps of succession categories for the beach plain study site on the Wadden island of Schiermonnikoog in 1959, 1970, 1978 and 1994. The categories represent different successional stages. Categories 1 and 2 are the youngest while 8 and 9 are the oldest.

has been indicated separately in Table 1 (not in Fig. 2). The dry dune sequence starts with pioneer species such as *Elymus farctus* and *Ammophila arenaria* and ends with vegetation dominated by shrubs and trees, mainly *Hippophae rhamnoides* and *Sambucus nigra*.

1952

The area consisted of a nearly bare sand flat, with scattered young dunes up to 2 m high. These dunes were sparsely vegetated with perennial grasses such as *Elymus farctus* and *Ammophila arenaria*. The lower parts were bare or sparsely covered with pioneer species such as *Salicornia europaea, Suaeda maritima* and *Glaux maritima*. The different vegetation types of the vegetation map of 1952 almost all belong to category 1 or 2 (99.4 %).

1959

Salt marsh vegetation, dominated by *Juncus gerardi* and *Festuca rubra* in which *Agrostis stolonifera, Armeria maritima* and *Schoenus nigricans* were frequent, developed in the southern parts of the area protected by dunes. *Hippophae rhamnoides* shrubs appeared on the higher dunes. The remaining part of the area has changed little since 1952. Most of the vegetation types belong to category 2, the remainder to categories 3 and 4.

1970

Ca. 33% of the area, predominantly in the centre, still had a vegetation cover of less than 25 %. A large part of the lower area was covered with pioneer vegetation composed of species such as *Salicornia europaea, Suaeda maritima, Glaux maritima, Agrostis stolonifera* and *Puccinellia distans*. Brackish dune slack vegetation with *Parnassia palustris*, *Salix repens* and *Juncus articulatus* started to develop in the westernmost part of the plain. Vegetation types with *Juncus gerardi* and *Festuca rubra* were expanding throughout the area and *Scirpus maritimus* appeared at low densities. Vegetation types dominated by *Festuca rubra, Hippophae rhamnoides* and *Chamerion angustifolium* started to colonise the dunes. Along the western edges of the beach plain, vegetation composed of *Sambucus nigra* and *Hippophae rhamnoides* appeared. The map based on categories ranging from 1 to 8 shows that the lower value categories were grouped around the middle of the beach plain and the higher value categories were distributed along the edges and in the western part of the study site.

1976

Areas with a plant cover of less than 25 %, decreased to 15 % of the total area of the study site; such locations were located mainly in the east. The brackish dune vegetation in the west and the vegetation types with *Juncus gerardi* and *Festuca rubra* in the centre expanded, *Juncus maritimus* started to colonise the lower parts and *Sambucus nigra* established on the higher dunes along the southern edge.

1978

The vegetation was comparable with that of 1976. A further decrease in the area of bare ground to 10 % of the total area occurred. *Scirpus maritimus* increased in the depressions. The map shows a strong decrease in categories 1 and 2 compared to 1970. A large part of the total area consisted of category 3. The western part mainly consisted of the categories 5, 6 and 7. The highest category (8) was found along the southern edges.

1994

Vegetation with a cover of less than 25 % again increased to 20 % of the area, especially in the eastern sections near the opening in the dike and also in the middle of the beach plain. In the eastern section a community with *Glaux maritima* was dominant. In some of the lower central parts pioneer species such as *Suaeda maritima* and *Salicornia europaea* were abundant. In the more western parts of the site the lowest areas were dominated by *Juncus maritimus* or *Phragmites australis* and/or *Scirpus maritimus*. Vegetation types characterized by *Juncus gerardi* and *Festuca rubra* were still abundant but decreased in the area compared to 1978. In the westernmost part the brackish vegetation with *Schoenus nigricans* was still present but scrub encroachment occurred and some trees of *Salix pentandra* and *Betula pendula* appeared. Most dunes were covered with a dense shrub vegetation of *Hippophae rhamnoides* and *Sambucus nigra* together with *Chamerion angustifolium* and *Calamagrostis epigejos*. Categories 1 and 2 increased compared to the values of 1978 especially in the centre and near the opening. Categories 3 and 5, the mid-successional stages, decreased. Most of the other categories, representative of the late successional stages, increased.

Temporal and spatial distribution of the vegetation categories

The percentage area occupied by the different vegetation categories between 1952 and 1994 is shown in Fig. 3. Category 2, representing a pioneer vegetation type, decreased between 1952 and 1978, but then increased again in 1994. Categories 3 and 5, both resembling the mid-successional stages, increased until the end of the 1970s, and decreased thereafter. Categories 6 to 9, representing the older successional stages, all increased with time. No clear trend can be seen for category 4.

The variance map (Fig. 4) shows the progress of succession in time for the different parts of the beach

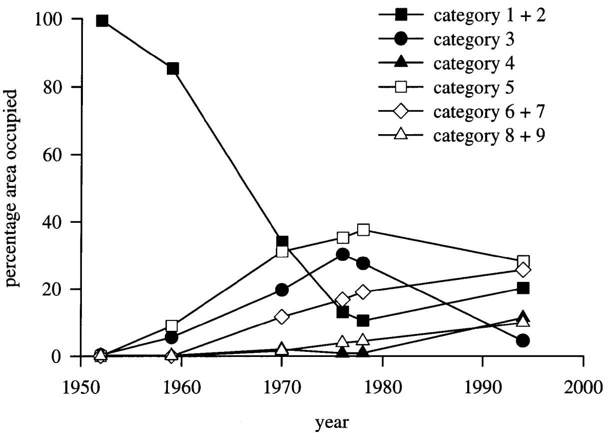

Fig. 3. The percentage of the total area occupied by vegetation categories 1-9 between 1952-1994 for the beach plain study site on the Wadden island of Schiermonnikoog.

plain. Examples of different sequences of categories, ranging from 2 to 9, and their variances are given in Table 2. Its shows examples of low variance (examples 1, 2 and 3), moderate variance (examples 4, 5 and 6) and high variance (examples 7, 8 and 9). It also demonstrates that it is not possible to distinguish between slow succession or areas which have been returned to an earlier successional stage as a result of disturbance (examples 4 and 5). The variance map (Fig. 4) shows the variance divided into six classes, the first class has a variance of zero, the other classes are divided into five equal parts ranging from zero to the maximum variance (9.77). Fig. 4 shows that less than 10 % of the study area has a high variance (dark grey and black), mostly along the edges, reflecting a major vegetation change. Almost 60 % of the area has a moderate variance (middle grey) indicating a moderate rate of successional change or a setback in succession. It includes most of the western part of the area and parts along the edges and the centre of the beach plain. One third of the area has a low or even a zero variance (light grey), indicating a minor vegetation change or no change at all. These areas are mainly situated near the gap in the eastern part and centre of the beach plain.

Table 2. Examples of different sequences of categories ranging from 2 to 9, exemplifying early to late successional stages for a beach plain succession on the Wadden island of Schiermonnikoog. For each sequence, the calculated mean and variance and the given class of variance are given.

Example	Sequence of category numbers	Average	Variance	Class
1	2 → 2 → 2 → 2 → 2 → 2	2.00	0.00	1
2	2 → 2 → 3 → 2 → 3 → 2	2.33	0.27	2
3	2 → 2 → 3 → 3 → 4 → 4	3.00	0.80	2
4	2 → 3 → 4 → 5 → 6 → 7	4.50	3.50	3
5	2 → 4 → 6 → 2 → 4 → 6	4.00	3.20	3
6	2 → 3 → 5 → 5 → 6 → 8	4.83	4.57	4
7	2 → 2 → 4 → 5 → 7 → 9	4.83	7.76	5
8	2 → 2 → 3 → 5 → 8 → 9	4.83	9.36	6
9	2 → 3 → 4 → 6 → 8 → 9	5.33	7.87	6

Discussion

Labeling vegetation types with their successional age

Dividing the different vegetation types into categories of successional age was possible because of repeated vegetation recordings made in a relatively undisturbed part of the area between 1972 and 1989 (Olff et al. 1993). However, the increase of organic matter and associated nutrient pools in time may not have been the same over the whole area. Disturbance can delay succession if the organic layer is (partly) removed. Salinity and flooding may restrict plant growth or may even eliminate species. Since plants are the main source of organic matter, its build up can be restricted. Hence the absolute successional age of a vegetation type may be different in disturbed parts of the beach plain compared with types present along the permanent transects. However, the sequence of species in time in a particular environmental setting, should remain the same. Successional age should therefore be read as the relative successional age. Despite these drawbacks the calculation of percentage similarities was robust and categorization of the different vegetation types was feasible.

Reconstruction of the succession

Vegetation change over time indicates an overall shift towards older successional stages for the whole beach plain. It shows a decrease of the pioneer stages, an optimum phase for the mid-successional stages and an increase of the late successional stages over time. The lack of any such trend for category 4 may be related to the occurrence of these vegetation types on the unstable transitional zone between plain and dune. The sudden increase of pioneer stages (category 1 and 2) in 1994 and the resulting low variance in the central parts of the beach plain suggests a successional setback. This increase of the pioneer stages is associated with an increase of bare soil. The vegetation map of 1994 indicated three classes of bare soil, all classified in category 2. Two classes differ in terms of percentage cover, the third consists of bare soil with less than 20 % vegetation cover and with an organic layer of more than 1.5 cm thickness. This third type occupied 6.8 % of the area, mainly in the centre of the beach plain. The presence of

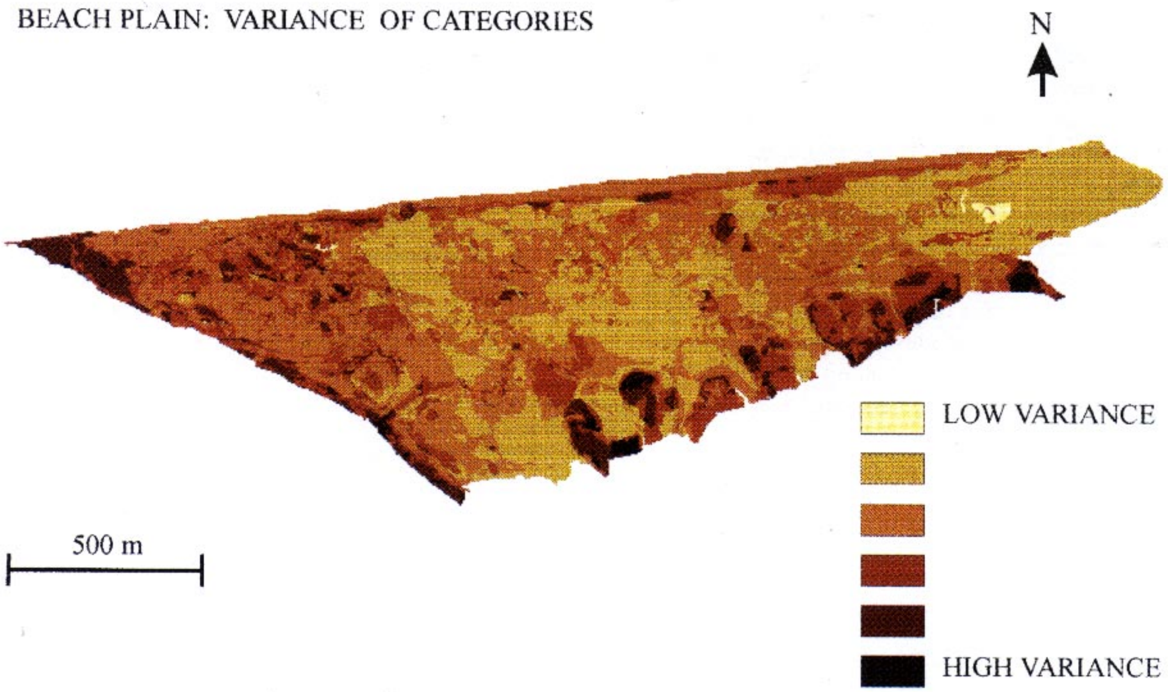

Fig. 4. Map showing the distribution of the calculated variance of sequences of categories ranging from 2 to 9 representing different successional stages, showing the progress of succession in time for the beach plain study site on the Wadden island of Schiermonnikoog. A low variance indicates a minor vegetation change, a high variance signifies a major vegetation change.

the organic layer indicates the previous existence of an older stage. Observations in 1989 suggested that these areas once were vegetated with *Juncus gerardi* and *Agrostis stolonifera* (van Tooren et al. 1993). These authors suggested that these two species died over a large area due to an inundation with salt water followed by a long dry period in 1989 which contributed to the development of hypersaline soils. Annual species such as *Salicornia europaea* and *Atriplex prostrata* recolonised the bare patches. Bare patches in salt marshes are often hypersaline due to increased surface evaporation in the absence of plant cover (Bertness et al. 1992; Srivastava & Jefferies 1995a). Patch colonization by competitive subordinates, which are relatively salt tolerant, appears to reduce substrate salinity by passively shading the substrate and as a result they may facilitate the invasion of a superior competitor (Bertness 1991). Thus a prolonged period of inundation with sea water, followed by a long dry period, can retard or halt succession. The dead remains may have been washed away by periodically strong water movements during winter. These strong water movements are probably also responsible for the exposure of the mineral substrate in some places. A similar setback has been reported from La Pérouse Bay in Canada (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995b). The formation of large 'peat barrens' produced as a result of grubbing (removal of roots and rhizomes of ground vegetation) by lesser snow geese (*Anser caerulescens caerulescens* L.) destroyed the sward and caused an increase in soil water salinity, thus preventing the re-establishment of vegetation.

The variance map shows that in a large part of the area (almost 33 %) succession was slow or undetectable (classes 1 and 2, Fig. 4). Less than 10 % of the area had a high succession rate (classes 5 and 6). The mid-range of the variance (classes 3 and 4) occupied the largest part of the area, almost 60 %. These results indicate that in a large part of the beach plain a very slow succession or even a setback of succession occurred. Thus inundation and salinity, together with the removal of top soil and/or sand burial during heavy storms have created a mosaic of vegetation types in the area. This zonation of different successional stages, created by disturbance, will probably remain for a long time if the present environmental setting of the beach plain as a whole does not change.

Implications for management

Our results show that stimulating natural dynamics in an area where coastal defence had led to a stabilization of wind and water movements may have a positive effect on biodiversity. The lack of management for an artificial sand dike has led to the formation of a tidal inlet (Dutch: slufter), where pioneer stages predominate, even in remote areas where succession had proceeded already for more than 20 yr. The exceptional combination of events (extreme flooding and periodically dry summers) eventually led to the almost complete removal of both vegetation and soil organic matter in certain areas. Consequently, a continuation of a less strict coastal defence policy in natural areas provides a good perspective for certain endangered pioneer species (Jansen 1995).

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