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Vegetation zonation in a former tidal area: A vegetation-type response model based on DCA and logistic regression using GIS

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Abstract. We studied the effect of flooding frequency on the vegetation of the northern part of the Delta region in the southwestern Netherlands under different grazing and soil conditions using Detrended Correspondence Analysis. We found grazing and frequency of flooding to be the most important environmental factors that determine zonation of vegetation types in the area. We used logistic regression to describe the probability of occurrence of 25 vegetation types in relation to the frequency of flooding under grazed and ungrazed conditions. We implemented the vegetation response model in a Geographical Information System so as to calculate new vegetation maps of outer dike areas under different flooding regimes. The model will be used for evaluation of the effects of different sluice management schemes on outer dike plant zonation in the research area.

Keywords: Flooding; Grazing; Modeling; Ordination; Wetland.

Nomenclature: van der Meijden (1990); Voous (1980).

Introduction

In 1970, the Haringvliet area, S.W. Netherlands (Fig. 1), was separated from the North Sea by a dam with 17 sluices. As a result, the daily water table fluctuations changed from ca. 1.5 m to 30 cm. This caused a notable change in vegetation of the outer dike areas. Salt and brackish plant communities disappeared within a few years, and were replaced by more productive vegetation types from freshwater areas. The drier soil conditions permitted grazing by livestock (cows, sheep and horses), and, to some extent, agricultural activity.

The Haringvliet area is part of the estuary of the rivers Rhine and Meuse (Fig. 1). This area comprises the Haringvliet and Hollandsch Diep, the Oude Maas, and the Nieuwe Merwede, and includes a wide range of hydrological conditions, land-use and substrates. We hypothesized that the differences in plant composition and relative abundance in this area can be explained by three major environmental factors: hydrology, land use and substrate.

Because the Oude Maas is still in open connection with the North Sea, it is hardly affected by the closing of the Haringvliet area. The tidal amplitude in this part of the area is 1.1 m. Therefore, the flooding frequency of outer dike areas is high, whereas the outer dike areas of the Haringvliet, at the same elevation, have a low flooding frequency. The effects of hydrology on vegetation zonation in tidal freshwater areas are well described by Zonneveld (1960) and de Boois (1982). Their studies of the Biesbosch before and after the closing of the Haringvliet both describe the importance of flooding frequency and/or duration for the vertical zonation of plant species and vegetation types. Similar results were found by Bren & Gibbs (1986) for river red gum forests.

Differences in land-use in the research area are mainly exhibited by grazing (cows, horses and sheep). In large parts of the outer dike areas along the Haringvliet, grazing is used as a management tool to create optimal habitats for hibernating geese (mainly *Anser anser*), and birds that prefer meadows for nesting, e.g. gotwit (*Limosa limosa*) and lapwing (*Vanellus vanellus*). Other areas along the Haringvliet and most of the areas along the Oude Maas and Nieuwe Merwede are ungrazed. Differentiation in grazing determines the striking differences in vegetation structure and species composition. In ungrazed parts of the research area, plant communities of tall herbs and shrubs are found, while in grazed areas different grassland communities can be distinguished. Thalen et al. (1987) presented a model to describe changes in vegetation structure and species composition under different grazing intensities.

In his extensive study of the Biesbosch, Zonneveld (1960) described differences in 'riverine' and 'estuarine' plant communities. According to this study, the differences between these two community types are the result of differences in soil texture; that is, clay soils in riverine - and sandy soils in estuarine habitats. Because of the large tidal influence in the Haringvliet and the Hollandsch Diep before the closing of the dam, soils are sandy compared to the soils of the Oude Maas and Nieuwe Merwede. Differences in plant composition due

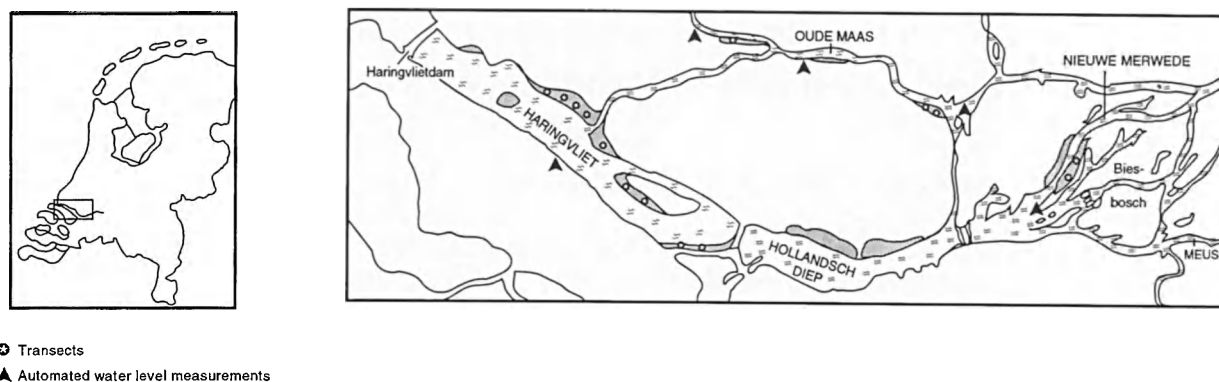


Fig. 1. Locations of outer dike areas, transects and automated water level measurements in the research area in The Netherlands.

to soil texture can be the result of differences in nutritional status of the soils and drainage capacity. Blom (1979) and Engelaar (1994) showed that soil compaction and differences in soil texture and mineral content are important factors for the growth of plants under both dry and wet soil conditions. To model the relationship between hydrology, grazing and soil texture and the occurrence of different vegetation types, we have to answer two questions: 1. What vegetation types can be distinguished in the research area? 2. How are these vegetation types related to hydrology, grazing and soil texture?

The ultimate goal of the research is to utilize sluice management of the Haringvliet as a steering factor for the succession of plant communities.

Material and Methods

Study area and vegetation data

Plant species composition changes from 'estuarine' to 'riverine', going from west to east in the Haringvliet area. The vegetation of the Oude Maas area is most similar to that described for 'De Biesbosch' (Zonneveld 1960; de Boois 1982), with plant communities of *Phragmites australis*, including *Caltha palustris* and *Cardamine amara*, and stands of *Scirpus lacustris* ssp. *tabernaemontani* and *S. maritimus*. The Hollandsch Diep/Nieuwe Merwede area has more species known from the upper reaches of the rivers Rhine and Meuse, e.g. *Senecio fluviatilis*, *Thalictrum flavum* and *Cuscuta europaea*. In this respect, the Haringvliet area takes an intermediate position. The vegetation of the outer dike areas of Haringvliet, Hollandsch Diep/Nieuwe Merwede and Oude Maas shows a distinct zonation of plant species and vegetation types perpendicular to the shoreline. Ungrazed areas are dominated by *Phragmites australis* and *Scirpus maritimus*, followed by vegetation with

Epilobium hirsutum and *Calystegia sepium*. *Rubus caesius*, *Althaea officinalis* and *Anthriscus sylvestris* are found on the highest places. In grazed parts, mainly in the Haringvliet section, the lower parts have vegetation with *Agrostis stolonifera* as the main grass species. Depending on grazing intensity higher parts are dominated by *Festuca arundinacea* with *Poa trivialis* (low grazing intensity) or *Lolium perenne* with *Poa trivialis* (high grazing intensity) as the main grass species.

In 13 outer dike areas (shaded areas in Fig. 1), the Survey Department of the Dutch Ministry of Public Works sampled 2294 plots at representative sites according to the Braun-Blanquet method (Westhoff & van der Maarel 1973), so-called relevés. We transformed the available cover/abundance scale data into a 1–7 scale for numerical analysis, hereafter referred to as data set A. This data set lacked important environmental data. Therefore, we sampled an additional 120 relevés in 14 line transects perpendicular to the shore, chosen so as to cross the most important vegetation types (Fig. 1). Data on type of management, elevation and soil characteristics were added to these relevés (data set B).

Elevation data

We determined the elevation of the relevés in data set A by overlaying relevé site maps to Digital Elevation Models (DEM), using the Geographical Information System GRASS4.0. The DEMs were constructed using local trend interpolation (Burrough 1987; Isaaks & Srivastava 1989) of elevation data taken from aerial photographs. Elevation was measured with leveling equipment (Wild NK2). For each relevé we averaged values of five measurements. All elevation data are relative to Amsterdam Ordnance Datum (mean sea level).

Hydrological data

Records of long-term automated measurements of water level (every 10 minutes over 15 - 20 yr) by the Ministry of Public Works provided important information on the relationship between elevation and flooding frequency. From these records, we determined cumulative frequency distributions of water levels. These values show how many times each water level was reached in the last 15 - 20 yr. We wrote a FORTRAN program to convert all elevation data into flooding frequencies. The relationship between elevation and flooding frequency differs across the research area. In the Oude Maas region, tidal influence diminishes from west to east; we therefore used interpolated data of three different locations. In the Haringvliet and Hollandsch Diep/Nieuwe Merwede areas, the relationship between elevation and flooding can be considered constant; for these two regions we used only one location per region (see Fig. 1).

Nature management data

At present, about 90 % of the outer dike areas in the research area are under control of nature conservation organizations, who provided the nature management data. The only form of active nature management in the research area is grazing by livestock. In the Haringvliet region approximately 50 % of the outer dike areas are grazed. In the Hollandsch Diep/Nieuwe Merwede and Oude Maas region, less than 5 % of the areas are grazed. We classified the relevés into three categories, based on nature management maps: heavy grazing (2 - 3 animals/ha), light grazing (0.1 - 0.2 animals/ha), and not grazed.

Soil data

For data set B we took soil samples from locations representative of vegetational zones. On each of 68 sites we took two samples: 70-cm³ cores for measurements on soil volume basis and extra soil material for chemical analysis. The cores were taken in the mineral soil at a depth of 10 cm and transported in plastic bags. We determined soil fresh weight immediately after return from the field. After drying at 105 °C for 8 hr we determined soil dry weight and water and air content of the samples and calculated soil bulk density (Fitzpatrick 1986). We performed a granular analysis of all soil samples to determine soil texture and classified soil texture according to the USDA soil texture triangle (Anon. 1975). To find differences in nutritional status of the soil on different locations, we measured [NH₄⁺], [NO₃⁻], and total phosphorus concentration. We also measured [Cl⁻] to determine the current influence of salinity on species composition of the vegetation. For

the analysis of chemical parameters, we made soil extracts by shaking 10 grams of fresh soil in 100 ml (bidistilled) water for 2 hr. We measured the following ionic concentrations colorimetrically on a Technicon II Auto Analyzer: NH₄⁺ (Kempers & Zweers 1986), NO₃⁻ (Kamphake et al. 1967) and Cl⁻ (O'Brien 1962). Total phosphorus content was measured by Inductive Coupled Plasma Emission Spectroscopy on an ICP plasma 200 (Thermo Jerrell Ash). We determined pH of the extracts with a 'double junction' Amphel pH electrode (Hanna Instruments SpA, Woonsocket RI, USA).

Modeling procedure

For classification of data set A we used TWINSpan, followed by agglomerative clustering using FLEXCLUS (van Tongeren 1986). We chose the Similarity Ratio as index of similarity (van Tongeren 1987) with a threshold value of 0.70. This threshold value may help finding clusters at the subassociation level (Westhoff & van der Maarel 1973). We analyzed data set B by direct gradient analysis using Canonical Correspondence Analysis (CCA) (ter Braak 1986, 1987a). After classification and selection of vegetation types to be used in the model, we combined the relevés of data set A with data set B (data set AB). We analyzed data sets A and AB by Detrended Correspondence Analysis (Gauch et al. 1974; ter Braak 1987b; Whittaker 1987). We considered the unimodal response model (Gauch & Chase 1974; Gauch et al. 1974; ter Braak & Looman 1986; Kooijman 1977; Austin 1987; Austin & Gaywood 1994) of DCA to be the most appropriate for the description of changes in the vegetation along the environmental gradients (Aitchison 1983; Pielou 1984; Eilertsen et al. 1990). Linear regression was used to describe the relationship between second axis scores of data set AB and the frequency of flooding of relevés. To integrate the clustering results with the ordination results, we used logistic regression (McCullagh & Nelder 1983; Anon. 1989) to describe the probability of occurrence of vegetation types, not individual species, to different combinations of nature management practices and flooding frequencies. Field observations indicate that vegetation types, like individual species, will show a unimodal response toward flooding frequency. Large clusters will have higher probabilities of occurrence than small ones, and clusters with a narrow range will have higher probabilities of occurrence in this particular range than clusters with a broad range. We assigned membership values to each relevé in the data set for the regression of grazed and ungrazed relevés to first axis DCA scores. Heavily grazed relevés received membership value 1 for the group of 'heavy grazing' and membership values 0 for both the groups light grazing and not grazed. We found

that using the light-grazing relevés separately in the analyses gave very poor results. A low number of relevés in combination with a broad range of occurrence on the first axis, gave a unimodal response curve almost completely encompassed by the response curves of the ungrazed and heavily grazed relevés. We therefore decided to split this group of relevés based on the results of the logistic regression. For the logistic regression of vegetation types to second DCA axis scores, each relevé belonging to a given cluster was assigned membership value 1 for that cluster, and membership value 0 for all of the other clusters. We analyzed each cluster separately. Based on visual inspection of the distribution of data points, we fitted first and second order polynomial models to the logit transformed membership data (ter Braak & Looman 1986, 1987), using the SAS logistic procedure (Anon. 1989):

$$\logit(p) = \ln(p/1-p) = aX + C \quad (1)$$

$$\logit(p) = \ln(p/1-p) = aX + bX^2 + C \quad (2)$$

Eq. 3 shows the general formula for the probability of occurrence:

$$p = \frac{e^{aX+bX^2+C}}{1 + e^{aX+bX^2+C}} \quad (3)$$

Eq. 3 is a Gaussian logit curve when parameter b is significantly smaller than zero. If parameter b is zero, then Eq. 3 describes a sigmoid (loglinear) response curve.

In all three models, p is the probability of occurrence at DCA score X , and a , b and C are maximum likelihood estimates of the regression parameters. The models that fitted best to the data, based on significance tests of the regression parameters and χ^2 tests of $-2 \ln L$ for the covariates X and X^2 , as well as visual inspection of the fitted curves to the original membership data, were chosen to be used in the vegetation response model (Trexler & Davis 1993).

GIS implementation

We used a Geographical Information System (GIS) for storage of vegetation and environmental data (Burrough 1986; Walsh et al. 1994) and displaying the modeling results. We chose GRASS4.0 (Westervelt 1991), a raster-based GIS with limited vector capabilities, to store vegetation maps, relevé locations, digital elevation models (DEMs) and nature management maps. We stored all relevé information (elevation, nature management, species composition and abundance, DCA scores etc.) in the relational database management system RIM (Fox 1990)

to be able to make specific selections on relevé characteristics.

Using the long-term water level measurements of the Oude Maas area, we transformed the digital elevation model of an outer dike area along the Haringvliet, on a cell-by-cell basis, into a flooding frequency map. Subsequently, we transformed this map into a second axis DCA score map, using the regression results of DCA scores to flooding frequency. For each vegetation type, we calculated a vegetation response map, showing the probability of occurrence of each type in each cell. We combined these probability maps to make a new vegetation map, taking for each cell in the map the vegetation type with the highest probability of occurrence. This predicted vegetation map is compared to the vegetation map under the present hydrological regime to show future changes in the Haringvliet according to the vegetation response model. Fig. 2 shows the GIS implementation of the vegetation response model.

Results

Classification

Classification of data set A resulted in 61 different vegetation units ranging from pioneer communities and grasslands to reed swamps, rough herbage communities and woodlands. We excluded the following vegetation types from the modeling procedure:

- Pioneer vegetation types with a total ground cover of less than 30 %. We consider these plant communities to be highly unpredictable because their species composition is highly variable in time and space.
- Woodlands, mostly willow coppices, planted for commercial purposes. These woodlands mostly have a separately regulated hydrological regime (Zonneveld 1960; de Boois 1982).
- Plant communities represented by clusters of less than 10 relevés. We found these vegetation types to be of little interest for the model because they appear at very specific combinations of environmental conditions and are therefore not representative of the entire research area.

The 25 vegetation units ultimately used in the modeling procedure are listed in Table 1. These units comprise ca. 80 % of the relevés in data set A.

Ordination

The DCA ordination of all relevés from data set A (Fig. 3) shows a distinct gradient of vegetation structure on the first ordination axis. The grassland communities are located on the left side of the diagram, while the

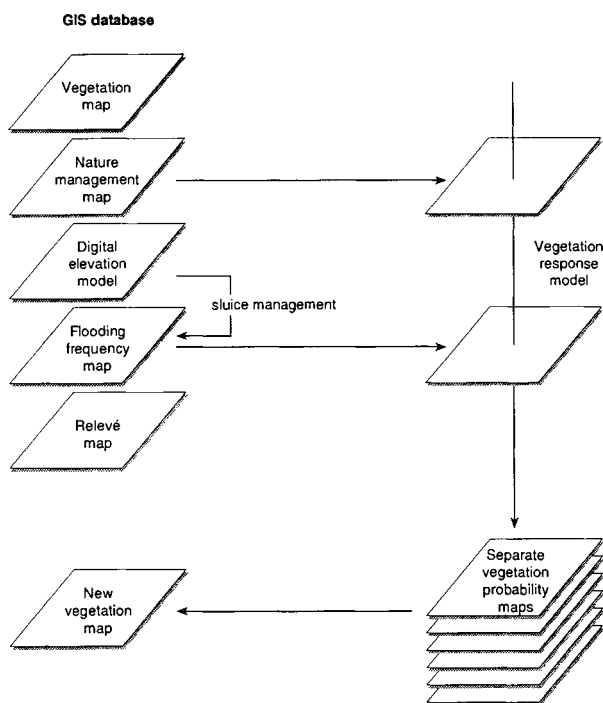


Fig. 2. Diagram of the GIS implementation of the vegetation response model. Maps from the GIS database are used as input for the model. The resulting vegetation maps can be saved into the GIS database for evaluation and further processing.

rough herbage communities and reed swamps are located on the right. The diagram also shows a gradient in soil moisture on the second ordination axis. At the lower part of the diagram, the moderately wet to dry communities are found. The vegetation units known from wet soil conditions are found at the upper part of the diagram.

The biplot (Gabriel 1971; ter Braak 1983; Thioulouse & Chessel 1992) of species and environmental variables of the CCA of data set B is shown in Fig. 4. The eigenvalues of the first and second axes are 0.63 and 0.40 respectively, explaining approximately 75% of the total variance. The biplot shows a strong correlation of heavy grazing (INT) and not grazed (NG), -0.72 and 0.71 respectively, with the first axis. Light grazing (EXT) is placed between the two extreme values of grazing intensity. Correlation coefficients for soil bulk density and total phosphorus content with the first CCA axis are -0.49 and 0.51 respectively. Soil texture (Sand, Silt, Loam and Clay) is only weakly correlated with the first axis (correlation coefficients: -0.40 , -0.21 , 0.31 and 0.44 respectively). Soil pH values and $[Cl^-]$ showed no differences between relevés and are therefore not shown. The flooding frequency of the relevés is strongly correlated with the second CCA axis (-0.83). Mineral nitrogen concentration (N), the sum of $[NH_4^+]$ and $[NO_3^-]$,

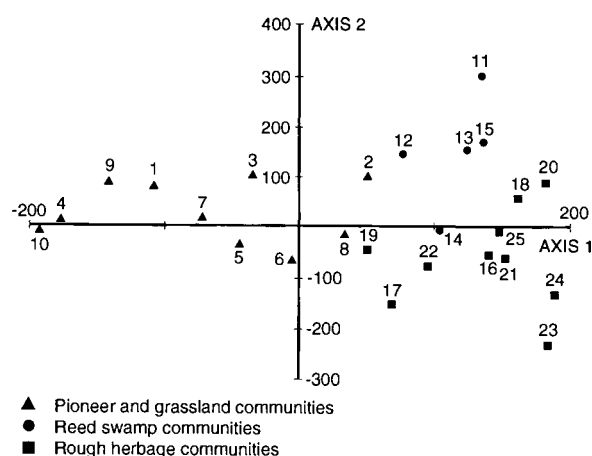


Fig. 3. DCA ordination of relevés from data set AB showing the distribution of vegetation structure on the first DCA axis. Only cluster centroids of vegetation types are shown in the graph. Cluster numbers correspond to those in Table 1.

also shows a (weak) correlation with the second axis: $r = 0.28$.

DCA ordination of the combined data set AB (1936 relevés) gave the following eigenvalues for the first and second axes: 0.62 and 0.46. We found a high correlation between the CCA scores of the data set B relevés and the DCA scores of these relevés in data set AB ($r = 0.85$ for axis 1, and $r = 0.82$ for axis 2). The B relevés cover the complete range of DCA scores in the combined data set AB. Data set B can therefore be regarded as a representative subset of data set AB. Pearson's correlation coefficient for grazing intensity of relevés with the first DCA axis is 0.66. The correlation of flooding frequency with the second axis scores of the relevés from data set B is 0.84. Note that these flooding frequencies are based on field measurements. The flooding frequency of the data set A relevés, derived from the DEMs, is very weakly correlated with the second DCA axis ($r = 0.16$). The ordering of species on the second DCA axis, however, shows a clear correlation with Ellenberg's (1979) moisture indicator values ($r = 0.61$). This suggests that axis 2 represents the 'wetness' of the vegetation in data set AB. We will discuss the discrepancy between the lack of correlation of data set A relevés with flooding frequency, and the good correlation of species scores with soil wetness, in the discussion section.

Regression results

Logistic regression of grazing intensity of relevés to the first DCA axis of data set AB shows a significant log-linear relationship (Fig. 5, Table 2A). Grazed relevés are mainly found at low axis scores, while ungrazed

Table 1. Description of the 25 vegetation units selected for the vegetation response model. The number of relevés in each cluster is given between brackets.

Open communities	
1.	Open vegetation with <i>Agrostis stolonifera</i> , <i>Polygonum lapathifolium</i> and <i>Juncus ambiguus</i> (12).
2.	Open vegetation with <i>Phragmites australis</i> and <i>Scirpus maritimus</i> (34).
Grassland communities	
3.	Grassland dominated by <i>Agrostis stolonifera</i> , with many annual- and 'saline' species (43).
4.	Grassland with <i>Agrostis stolonifera</i> , <i>Lolium perenne</i> and <i>Poa trivialis</i> (65).
5.	Grassland with <i>Festuca arundinacea</i> and <i>Ranunculus sardous</i> (91).
6.	Rough grassland with <i>Elymus repens</i> (13).
7.	Rough grassland with <i>Festuca arundinacea</i> and <i>Cirsium arvense</i> (85).
8.	Rough meadow with <i>Agrostis stolonifera</i> , <i>Poa trivialis</i> and <i>Cirsium arvense</i> (50).
9.	Grassland with <i>Agrostis stolonifera</i> and <i>Glaux maritima</i> (11).
10.	Meadow vegetation with <i>Lolium perenne</i> and <i>Poa trivialis</i> (169).
Reed swamp communities	
11.	Vegetation of <i>Glyceria maxima</i> with <i>Iris pseudacorus</i> (16).
12.	Vegetation dominated by <i>Scirpus maritimus</i> (16).
13.	Typical, almost monospecific reed swamp community of <i>Phragmites australis</i> (57).
14.	Community of <i>Phragmites australis</i> with <i>Calystegia sepium</i> (95).
15.	Reed swamp with <i>Phalaris arundinacea</i> , <i>Phragmites australis</i> and <i>Calystegia sepium</i> (33).
Rough herbage communities	
16.	Very typical rough herbage in the Haringvliet area with <i>Epilobium hirsutum</i> as the dominant species and <i>Calystegia sepium</i> (165).
17.	Rough herbage community with <i>Elymus athericus</i> , <i>Calystegia sepium</i> and <i>Phragmites australis</i> (50).
18.	Rough herbage with <i>Urtica dioica</i> and <i>Anthriscus sylvestris</i> (131).
19.	Vegetation of <i>Festuca arundinacea</i> , <i>Phragmites australis</i> and <i>Calystegia sepium</i> (45).
20.	Rough herbage with <i>Valeriana officinalis</i> , <i>Symphytum officinale</i> , and <i>Calystegia sepium</i> (25).
21.	Rough herbage with <i>Urtica dioica</i> , <i>Phragmites australis</i> and <i>Cirsium arvense</i> (27).
22.	Rough herbage with <i>Eupatorium cannabinum</i> and <i>Phragmites australis</i> (104).
23.	Rough herbage dominated by <i>Solidago gigantea</i> (56).
24.	Rough herbage with <i>Epilobium hirsutum</i> and <i>Rubus caesius</i> (60).
25.	Community of <i>Angelica archangelica</i> with <i>Phragmites australis</i> and <i>Epilobium hirsutum</i> (65).

relevés are found at high scores. The two lines fitted by logistic regression intersect at DCA score – 38. Based on this regression the data set was split into grazed and ungrazed relevés. 'Light grazing' relevés with first axis scores lower than or equal to – 38 were assigned to grazed vegetation types and relevés with scores higher than – 38 were assigned to ungrazed vegetation types. Due to this division three vegetation types, typical to lightly grazed conditions were split (units 5, 6 and 7, Table 1).

The wetness of the soil, as represented by the second axis DCA scores of relevés, is highly correlated with the

frequency of flooding for the relevés of data set B. We found a good fit ($R^2 = 0.75$) for the linear regression of relevé scores to the square root of flooding frequency (Fig. 6). The elevation data of data set A, derived from aerial photographs, gave very poor results (see Discussion).

The results of the logistic regression of second axis relevé scores of grazed and ungrazed vegetation types are shown in Table 2B and Figs. 7 and 8. For most of the plant communities we only found unimodal response curves (second order model) to fit well to the data. For some vegetation types, however, a good fit was found using a log-linear (first order) response model. For these communities, the second order model parameters values are given as blanks in Table 2B, indicating values not significantly smaller than zero. The results suggest that, if optima exist for the clusters 13, 16 and 23, these lie outside the range of the second DCA axis of the data set. Blank first order parameters indicate curves with a response curve optimum near DCA score zero. These curves, units 14 and 25, do have second order parameters significantly smaller than zero, and therefore show a unimodal response. For some vegetation types, the maximum probability of occurrence is very low. This especially applies to vegetation types with a low number of relevés and a broad range of occurrence on the second DCA axis. For the sake of clarity of Figs. 7 and 8, response curves of vegetation types completely encompassed by other curves are not shown. Therefore, although separate vegetation response maps of these vegetation types can be calculated by the model, these communities will not be found in the ultimate, combined vegetation map.

GIS implementation

Fig. 9a shows the flooding frequency map of an outer dike area at the northern border of the Haringvliet under the present sluice management scheme. We created this map by replacing the elevation data in the digital elevation model by their respective flooding frequencies. The sluices in the Haringvliet dam are only opened when sea water level is low. Therefore, the mean tidal amplitude of the Haringvliet is only 28 cm, with a mean low water level of 36 cm and a mean high water level of 64 cm. As can be seen in Fig. 9a, most of the outer dike area is seldom flooded (yellow and green parts). In the Oude Maas area, the mean low water level is – 11 cm. The mean high water level is 95 cm. This flooding scheme applied to the aforementioned outer dike area along the Haringvliet is shown in Fig. 9b. The flooding characteristic is comparable to a sluice management scenario of permanently opened sluices.

The effects of this scenario on the distribution of

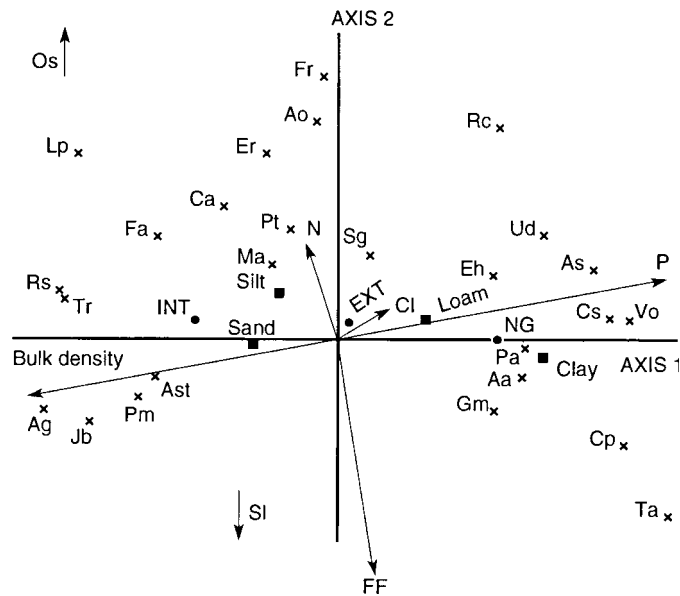


Fig. 4. CCA biplot of plant species and environmental variables from data set B. Continuous variables are represented by arrows (ter Braak 1987a). Ordinal variables are represented by dots (nature management) and squares (soil texture): FF = flooding frequency; Cl = Chloride; N = Total nitrogen; P = Total Phosphorus; INT = heavy grazing; EXT = light grazing; NG = not grazed. Most characteristic species are shown:

Aa = *Angelica archangelica*; Ao = *Althaea officinalis*;
 Ag = *Alopecurus geniculatus*; As = *Anthriscus sylvestris*;
 Ast = *Agrostis stolonifera*; Ca = *Cirsium arvense*;
 Cp = *Caltha palustris*; Cs = *Calystegia sepium*;
 Eh = *Epilobium hirsutum*; Er = *Elymus repens*;
 Fa = *Festuca arundinacea*; Fr = *Festuca rubra*;
 Gm = *Glyceria maxima*; Jb = *Juncus bufonius*;
 Lp = *Lolium perenne*; Ma = *Mentha aquatica*;
 Os = *Ononis spinosa*; Pa = *Phragmites australis*;
 Pm = *Plantago major*; Pt = *Poa trivialis*;
 Rc = *Rubus caesius*; Rs = *Ranunculus sardous*;
 Sg = *Solidago gigantea*; Sl = *Scirpus lacustris*;
 Ta = *Typha angustifolia*; Tr = *Trifolium repens*;
 Ud = *Urtica dioica*; Vo = *Valeriana officinalis*.

vegetation types are shown in Figs. 9c and 9d. Fig. 9c shows the vegetation map as calculated by the model under present sluice management, Fig. 9d shows the predicted vegetation map with permanently opened sluices. Nature management is not changed in this example. A clear shift can be seen in the zonation of vegetation types perpendicular to the shore line. The area of the reed swamp community of unit 15 (*Phalaris arundinacea*) increases from 1.6 to 51 acres, and the rough herbage community of unit 22 (*Eupatorium cannabinum*) is largely replaced by unit 18 (*Urtica dioica*). The grassland community dominated by *Agrostis stolonifera* increases from eight to 42 acres. It is to be noted that the change in vegetation distribution is not simply a matter of replacing one community by another. As can be seen in Figs. 9c and 9d, the vegetation pattern is completely different.

Discussion

Ordination and regression

We found that the most prominent differences in the three data sets used in the analyses are related to grazing and hydrology, not to soil texture. Soil texture could not satisfactorily be fitted to any of the first four ordination axes, neither in DCA, nor in CCA. The only soil parameters with high correlations with the first axis are phosphate and soil bulk density. The latter is a result of trampling of the soil by cattle (see also Engelaar 1994). We argue here that the correlation of phosphate with the first ordination axis is an artefact of grazing.

Phosphate is a very abundant nutrient in river areas (Mitsch & Gosselink 1986). Although both Haringvliet and Oude Maas are mainly fed by the river Rhine, marked differences can be found in soil phosphate concentrations; in the Oude Maas area soil phosphate concentration is higher than in the Haringvliet area. This is partly due to the absence of grazing in the Oude Maas area, causing accumulation of phosphate, and partly to the high clay content of the soil along the Oude Maas as phosphate is strongly retained by clay particles (Mitsch & Gosselink 1986). Given the fact that phosphate is not limiting in any part of the research area, we think that differences in vegetation structure are not caused by high phosphate concentrations, but that high phosphate concentrations are correlated with differences in vegetation structure. This

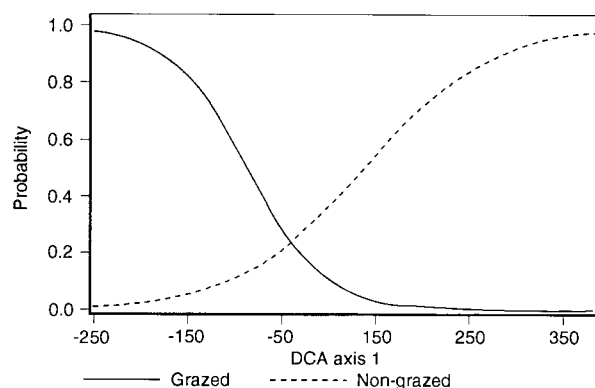


Fig. 5. Logistic regression curves of nature management to first DCA axis relevé scores.

Table 2. A. Logistic regression parameters and model fit of nature management to the first DCA axis scores of relevés. Parameter values shown are significantly different from zero ($p < 0.05$); those not significantly different from zero are indicated with -. N = number of relevés; L = Likelihood ratio (Trexler and Travis 1993). **B.** Ibid. of the relevé scores of 25 vegetation units to the second DCA axis.

		Regression parameters			Criteria for model fit	
		N	Intercept	Axis ₁	$-2 \ln L$	χ^2 (df)
A.						
Grazed		565	-0.79	-0.02	1291.39	959.69
Ungrazed		1233	0.69	0.02	1333.49	943.85
B.						
Grazed units						
	N	Intercept	Axis ₂	Axis ₂ ²	$-2 \ln L$	χ^2 (df)
1	12	-12.33	0.25	-0.0010	69.56	47.60 (2)
3	43	-4.17	0.06	-0.0002	192.16	115.55 (2)
4	65	-1.50	0.03	-0.0008	359.39	49.45 (2)
5	91	-1.57	-0.03	-0.0003	450.94	55.77 (2)
6	13	-9.51	-0.21	-0.0001	69.41	55.41 (2)
7	85	-1.50	0.02	-0.0003	450.36	35.51 (2)
9	11	-9.63	0.15	-0.0007	65.64	43.69 (2)
10	169	0.19	-0.04	-0.0002	490.35	215.04 (2)
Ungrazed units						
2	34	-7.77	0.12	-0.0005	215.96	94.94 (2)
5	57	-2.88	-0.04	-0.0003	368.51	92.70 (2)
6	23	-4.10	-0.04	-0.0002	192.20	36.31 (2)
7	18	-3.22	0.02	-0.0003	157.25	30.48 (2)
8	50	-1.99	-0.01	-0.0003	343.92	74.04 (2)
11	16	-19.07	0.11	-0.0002	68.07	102.59 (2)
12	16	-12.42	0.13	-0.0004	113.62	57.05 (2)
13	57	-3.67	0.01	-	365.99	95.22 (1)
14	95	-2.10	-	-0.0003	647.31	21.24 (1)
15	33	-7.24	0.06	-0.0001	205.27	98.48 (2)
16	165	-1.95	-0.003	-	949.61	19.24 (1)
17	50	-6.75	-0.06	-0.0001	304.85	113.11 (2)
18	131	-1.79	0.02	-0.0001	692.404	141.21 (2)
19	45	-2.68	-0.008	-0.0001	354.73	31.11 (2)
20	25	-4.30	0.03	-0.0001	204.24	39.92 (2)
21	27	-3.66	-0.01	-0.00005	245.93	13.56 (2)
22	104	-2.48	-0.025	-0.0001	592.95	119.96 (2)
23	56	-6.3	-0.02	-	240.59	214.56 (2)
24	60	-3.95	-0.023	-0.00006	403.81	75.36 (2)
25	65	-2.01	-	-0.0001	453.31	55.11 (1)

should be noted when interpreting ordination biplots such as Fig. 4.

We find differences in vegetation structure on the first ordination axes of all three data sets. These differences are highly correlated with grazing. At high grazing intensities, grasslands are found, while at ungrazed parts communities of tall herbaceous species occur, in particular rough herbage communities and reed swamp vegetation types. Intermediate grazing leads to mixed communities of grasslands and shrubs (see also Gordon 1989a, b). Because intermediate grazing only gave low probabilities of occurrence to the first axis scores, and most relevés of

these vegetation types had high similarities to ungrazed communities, we assigned most of these relevés to ungrazed vegetation types in the final model.

The second ordination axis reveals a good correlation with soil wetness. This is supported by the ranking of species of all three data sets, as well as by the CCA analysis of data set B and the regression of a subset of data set AB, where elevation was determined by field measurements. Most of the total variance on this axis can be explained by the frequency of flooding. We expect that in very frequently flooded parts of the outer dike areas, the duration of flooding and the frequency of drainage become more important (van der Sman et al. 1988). The scatter plot of Fig. 6 shows a slight tendency to bend upwards at frequently flooded relevés, suggesting that differences in plant composition are not only due to the frequency of flooding. For the regression of flooding frequency to the second DCA axis scores of relevés, we used square root-transformed data, not only because the model fit was better, but also because we think that this model is conceptually better. At low flooding frequencies, other factors will become increasingly important for changes in second axis scores. The lack of correlation of the data set A relevé scores with flooding frequency derived from DEMs can be explained by the fact that the quality of current DEMs is low. This applies especially in ungrazed areas, where thick piles of dead plant material (up to 50 cm) can be found as floodmarks. DEMs should be derived from field measurements, not from aerial photographs.

Although ordination by DCA is not undisputed (e.g. Wartenberg et al. 1987; Peet et al. 1988; Tausch et al. 1995), we find that the results presented here correspond well to field observations and with what is generally known of the effects of grazing to vegetation structure (e.g. van Andel & van den Bergh 1987; Gordon 1989a, b) and of the effects of flooding on plant zonation (Blom et al. 1990; Voeselek 1990).

Interactions between grazing, flooding and soil conditions

Grazing not only causes the removal of plant biomass (van Andel & van den Bergh 1987), giving marked differences in vegetation structure (Gordon 1989a, b), but also trampling of the soil. Trampling causes gaps in the pasture, especially under wet soil conditions. These gaps (safe sites; Pacala & Silander 1985) are suitable places for annual species to germinate and emerge (Gibson & Brown 1991). In the research area, species known from former brackish habitats such as *Juncus gerardii*, *Juncus ambiguus*, *Glaux maritima* and *Spergularia salina*, are still found in these gaps, although $[Cl^-]$ is low. Westhoff & Sýkora (1979) also found that after 33 yr of desalination

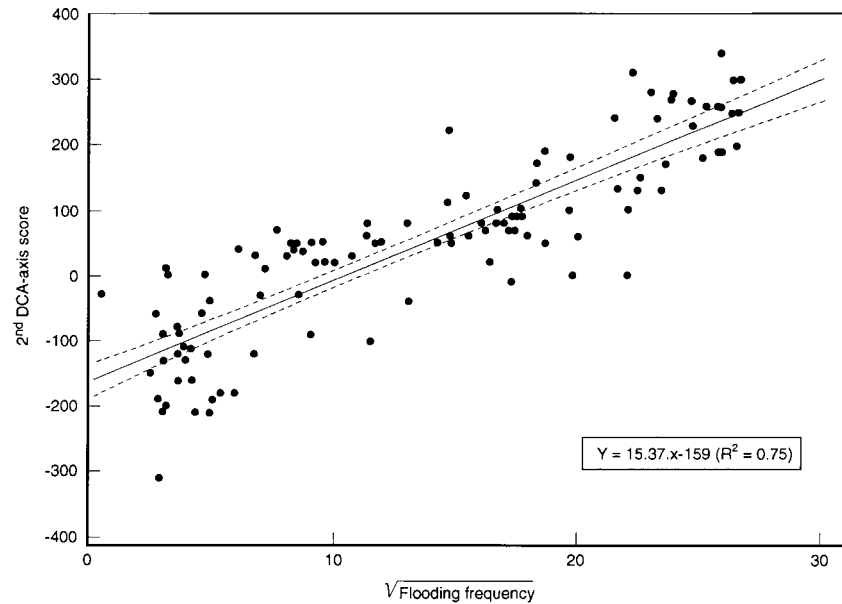


Fig. 6. Linear regression of scores of 120 B relevés on the second DCA axis to the square root of flooding frequency.

in the former Zuiderzee area, species from the class *Asteretea tripolii* were still found in grazed areas, while in ungrazed areas all 'saline' species had disappeared. Gap creation by grazing cattle is probably a prerequisite for the survival of these species in the future of the Haringvliet area. Another important effect of grazing by cattle is soil compaction (Blom 1979). Engelaar (1994) found that soil compaction can cause hypoxic conditions in the soil, comparable to the effects of flooding, because diffusion of oxygen into compacted soils is hampered. We found marked differences in soil air-filled pores between locations separated over a distance of only 1 m (data not shown). One location was situated on a cattle track, the other was not. Hypoxic soil conditions due to soil compaction cannot be distinguished from those caused by flooding, although species composition could be influ-

enced by this hypoxia.

Effects of flooding on individual plant species have been extensively studied. Flooding-tolerant plants can have different adaptations to flooding: aerenchyma formation in the roots (Laan et al. 1989), petiole elongation (Voesenek & Blom 1989) or life-history adaptations (van der Sman 1992; van der Sman et al. 1992). These adaptations are especially important where prolonged inundations occur. In the research area, these conditions can be found in seldomly drained places under mean low water level, but also in places where soil conditions do not allow percolation of water because of the high clay content. In the latter case, places with a low flooding frequency can show wet vegetation types (Zonneveld 1960). Unfortunately, present DEMs are not accurate enough to reveal these depressions in the landscape.

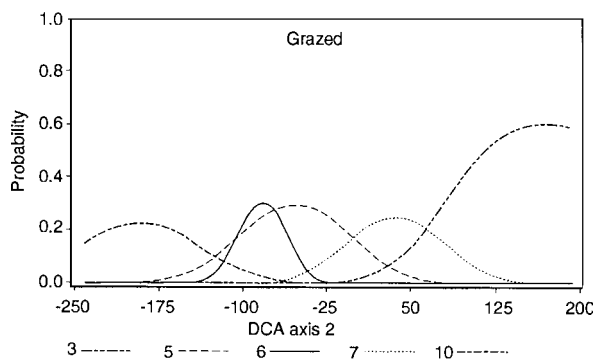


Fig. 7. Logistic regression curves of grazed vegetation types to second DCA axis relevé scores.

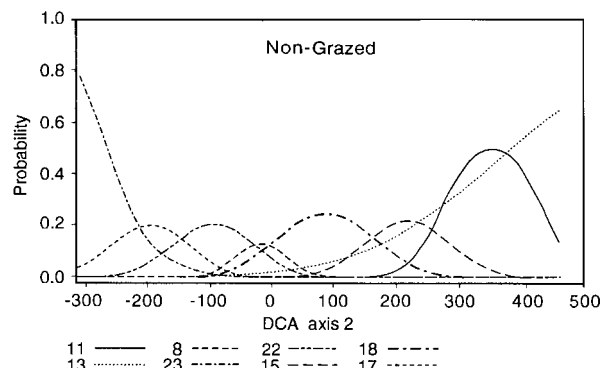


Fig. 8. Logistic regression curves of ungrazed vegetation types to second DCA axis relevé scores.

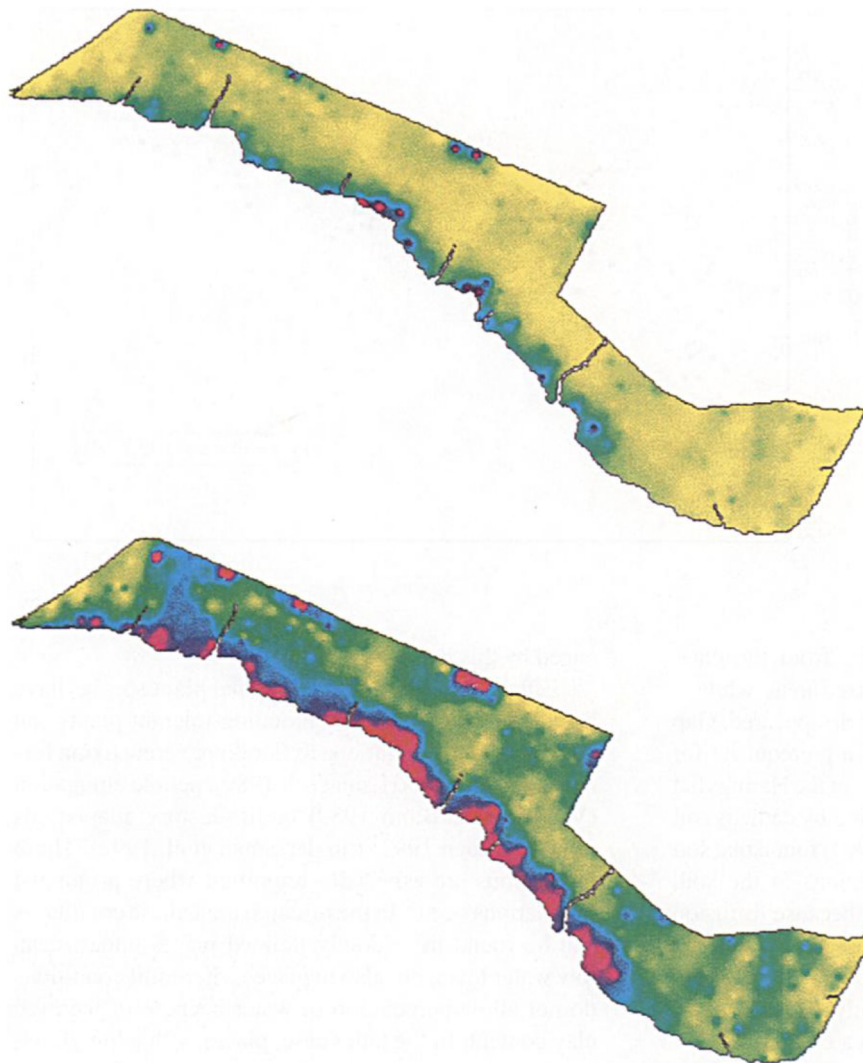


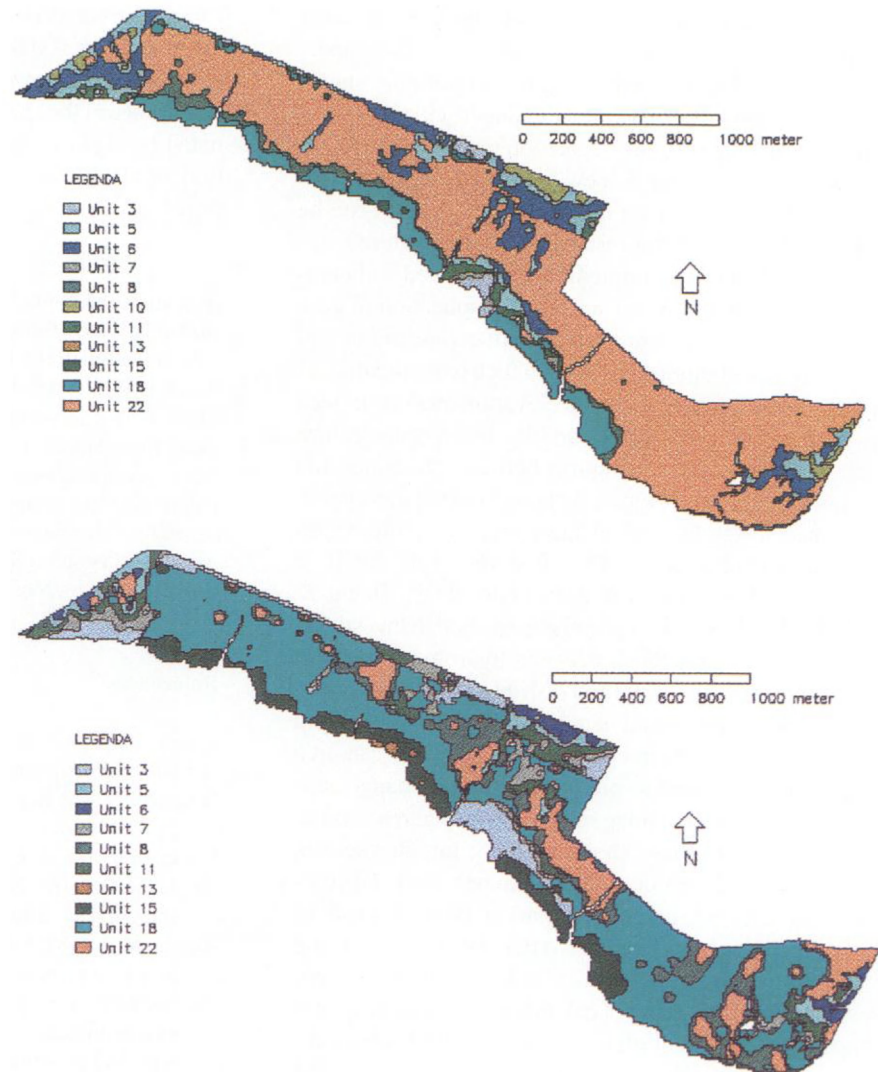
Fig. 9. **a.** Flooding frequency map of the 'Beninger Slikken' (Haringvliet) under present sluice management. Maximum flooding frequency is 706 times per year. **b.** Calculated flooding frequency map corresponding to permanently opened sluices. Pixel values: red>blue>green>yellow.

Modeling

A good ordering from wet to dry vegetation types can be found on the second axis. When this ordering is compared to field observations, however, some marked differences are found: the monospecific vegetation type of *Phragmites australis* can presently be found as a narrow strip along the shore lines of the Haringvliet area. According to the model (unit 13 in Fig. 8), this vegetation type can hardly be found under the present sluice management regime (see Figs. 9a, c), because it is almost completely encompassed by units 15 (*Phalaris arundinacea*) and 11 (*Glyceria maxima*). Both these units are mainly found in 'riverine' habitats along Oude Maas and Nieuwe Merwede, while unit 13 (*Phragmites australis*) is a typical 'estuarine' plant community. This

could mean that the vegetation along the Haringvliet is still in motion, i.e. changing from an estuarine to a riverine system. Zonneveld (1960) found differences between 'riverine' and 'estuarine' habitats to be related to differences in soil texture (clay soils vs. sandy soils). These differences in soil texture could not be found to play an important role in the study presented here. What we do find, is that the three vegetation types can be clearly separated by their third DCA axis scores. Unfortunately, none of the environmental parameters we determined could be satisfactorily related to the third ordination axis. The vegetation dominated by *Epilobium hirsutum* (unit 16), another very typical community in the Haringvliet area, is completely encompassed in the model by the *Solidago gigantea*-dominated community. A possible explanation for the fact that unit 16 is pres-

Fig. 9c. Vegetation map corresponding to flooding frequencies shown in Fig. 9a. For descriptions of the vegetation units see Table 1. **d.** Predicted vegetation map corresponding to flooding frequencies shown in Fig. 9b. See Table 1 for descriptions of the vegetation units.



ently typical in the Haringvliet area, is that it was there first. Apparently, conditions for germination immediately after the closing of the Haringvliet dam were very suitable for *Epilobium hirsutum*, allowing this species to invade areas where large stands of *Phragmites australis* had collapsed. Although represented by a large number of relevés, this community is present over such a broad range of flooding frequencies that no real optimum could be found. This could mean that the present vegetation of *Epilobium hirsutum* is a temporary successional stage in the Haringvliet area; this is supported by field observations in the summer of 1994. Places that were predominantly occupied by *Epilobium hirsutum* in 1991, are now dominated by *Solidago gigantea*, a strongly expanding neophyt in the research area. Extrapolation of the model to DCA scores lower than -300 predicts

this development. This would suggest that *Solidago gigantea* is a stronger competitor than *Epilobium hirsutum* under dry soil conditions (see also Shamsi & Whitehead 1974, and Cornelius 1990), and that vegetation types presently dominated by *Epilobium hirsutum* will be replaced by communities dominated by *Solidago gigantea* if hydrological conditions are not changed.

Implementation of the vegetation response model into a Geographical Information System has several advantages. First, all data from the research area are available in one database: maps, Digital Elevation Models and site maps of relevés. These data can easily be combined, retrieved, updated and used for different purposes (Burrough 1986). As a consequence of this, results from other models, e.g. newly calculated flooding frequency maps for different sluice management schemes, or new

nature management maps can easily be used as input maps for the vegetation response model. A second important aspect is that the vegetation model not only shows *what* will happen, but also *where* changes will take place. Thirdly, the results of the vegetation response model are immediately available as new vegetation maps so that effects of different sluice management scenarios can be compared. The fact that results of different nature management schemes can immediately be viewed and compared could be a step forward in the application of ecological models by nature management organizations and policy makers. Future research will focus on validation of the model by using new digital elevation models derived by laser altimeter (in prep.) and by incorporating third axis DCA scores to distinguish between 'riverine' and 'estuarine' vegetation types. Although not yet thoroughly evaluated in the ecological literature, fuzzy ordination (McBratney & Moore 1985; Roberts 1986; Feoli & Zuccarello 1988; Feoli & Zuccarello 1992; Zhang & Oxley 1994) looks like a promising method to investigate the effects of interactions between hydrology, land-use and soil texture on vegetation distribution.

The model presented here shows that ordination and classification results in combination with GIS can, to a large extent, be used to predict vegetation changes under different sluice management schemes and to immediately visualize these changes on a computer screen. Within hours, different schemes can be tested and compared. We chose to use vegetation types instead of individual plant species for two reasons. First, by using vegetation types we get a large reduction of data in our response model; instead of calculating separate response maps for all different plant species (ca. 200), we calculate only 25 response maps of vegetation types, saving much time and computer resources. Second, we think that vegetation types give better insight into environmental factors determining vegetation than individual species. Species such as *Urtica dioica* and *Phragmites australis* can occur under a broad range of environmental conditions, while the subassociations in which they occur as dominant species are very different in their associated species content under different conditions.

In this paper, we show that by opening more sluices and/or for a longer time-span, the tidal amplitude in the research area will increase, increasing the frequency of flooding of larger parts of the outer dike areas and consequently increasing the amount of wetlands. According to the model, *Urtica dioica*-dominated communities will disappear when outer dike areas are flooded more than 400 times per year, which is in accordance with Zonneveld's (1960) observations who finds *Urtica dioica*-dominated vegetation types to be correlated with well aerated places. The probability of occurrence of reed swamp vegetation with high abundance of

Phragmites australis increases strongly at flooding frequencies over 100 times per year. Flooding frequencies over 100 times per year also increase the probability of occurrence of the species-rich grassland vegetation dominated by *Agrostis stolonifera*, the replacement vegetation of *Phragmites* communities under grazed conditions.

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