



Evaluation of changes in permanent plots in the dunes and upper salt marsh at Ameland East

Ecological effects of gas extraction

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Inhoudsopgave

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Abstract

On the West Frisian island of Ameland (The Netherlands), natural gas has been extracted since 1986. This has caused a soil subsidence of c. 1-30 cm. In order to monitor the effects of soil subsidence on the vegetation, permanent plots were installed at the start of the gas extraction and monitored at three-year intervals up to 2001. In a statistical analysis it was attempted to relate the vegetation of the plots to measured environmental variables and their changes. The following environmental variables were measured: elevation, groundwater level, flooding frequency, and soil chemistry. It was attempted to interpret the changes in the vegetation on the basis of (a) the spatial pattern of vegetation and environmental variables at the start of the monitoring, and (b) the changes in the environmental variables over time. The hypothesis was tested that the temporal change is a reflection of the spatial pattern i.e. the vegetation responds to a change in an environmental variable by becoming more similar to the vegetation in a site where the 'new' value of this environmental variable was already present at the start of the monitoring. This hypothesis appeared to be true for part of the changes in the vegetation, namely those caused by changes in flooding frequency and groundwater level. The changes in flooding frequency and groundwater level were in turn caused by a combination of weather fluctuations and soil subsidence, and therefore consisted of superimposed monotonous and oscillatory signals. However, an important trend in the vegetation was not related to any of the measured environmental variables (including soil subsidence). This trend can be interpreted as a tendency towards eutrophication. Its cause cannot be derived from our data, but a similar trend is reported in many sites in the dunes of the Netherlands and adjacent countries.



1. Introduction

Extraction of natural gas leads to compaction of the geological formations in which the gas is located. When this compaction is transported upwards it will ultimately lead to subsidence of the soil level. A typical value for subsidence is c. 10-30 cm when a medium-sized gas field is completely drained. Although the ecological effect of soil subsidence is generally limited, strong effects may be expected in coastal areas. Here the vegetation is mainly determined by the balance between saltwater and freshwater, which may be affected by even small changes in soil surface level. The aim of the present study is to estimate the effect on dune and upper salt marsh vegetation of progressive soil subsidence (up to c. 30 cm), occurring over a 15-year period on the West Frisian island of Ameland (The Netherlands).

Ameland (53°27'30"N 5°53'00"E) is part of the chain of barrier islands that are located along the coasts of The Netherlands, Germany and Denmark, and that separates the Wadden Sea from the North Sea. Most of these islands consist of a sandy dune landscape along the North Sea coast, and a clayey salt marsh landscape along the Wadden sea coast (Van Dieren 1934, Dijkema & Wolff 1983, Ketner-Oostra & Sýkora 2000). The salt marshes have partly been enclosed by dykes and are presently in agricultural use. However, the eastern part of Ameland, where our study was conducted, is open to the sea and has little human influence. In this area extraction of natural gas started in 1986. As it was expected that soil subsidence would lead to a significant loss of natural values in this reserve area, a monitoring program was set up before the start of the gas extraction. To this end, permanent plots were laid out of which the vegetation was described at three-year intervals. The present study evaluates the permanent plot observations that were made in 1986, 1989, 1992, 1995, 1998 and 2001.

In coastal environments a strong correlation is nearly always observed between the vegetation and the elevation of the soil surface. However, this correlation comes about only indirectly. Water level and salt influence are usually assumed to be the real key factors for the vegetation, and these are at least partly determined by the elevation. This means that changes in elevation lead to changes in at least two factors that directly influence vegetation. However, when the effect of changes in elevation over a relatively short period has to be evaluated (like in our case), weather conditions also have to be taken into account, as these can cause significant year-to-year changes in both freshwater and saltwater influence. Therefore we have the complicated situation that the two key factors that the vegetation directly responds to, are themselves determined by both weather conditions and soil surface level. Furthermore, the vegetation is also determined by factors like chemical composition and physical characteristics of the soil, that are less variable over time (and considered constant in the study). Here we attempt to separate the indirect effects of both weather conditions and elevation of the soil surface on the basis of their different behaviour in time, also taking into account the some of the soil characteristics that are constant over time.

For a vegetation consisting of hundreds of species, an evaluation of the quantitative change of every single species is not practically feasible. On the other hand an evaluation using vegetation types (either following a universal or national typology e.g. the system of Braun-Blanquet (1954); or using a local typology) is probably too coarse to show the subtle changes that took place during our monitoring. We therefore used the 'detrended' form of Correspondence Analysis (DCA; Jongman et al. 1995) as a method to summarise the spatial pattern and the temporal change in the vegetation, that is simple but still sensitive enough to reveal effects of soil subsidence. Besides we used the canonical form of Correspondence Analysis (CCA) to



characterise the effects of the various environmental factors (groundwater level; flooding frequency; and soil characteristics), and to make a ranking of their influence on the vegetation.

Besides characterising the changes in the vegetation per se, an important aim of the present study was to determine whether soil subsidence had caused any change in biodiversity. We used two measures to quantify biodiversity. The first is the number of species per plot, and the second is the 'Compound Conservancy Value' (CCV) described by Wamelink et al. (2003). This is a measure related to the criteria of the Red List (IUCN 2001), that attributes a value to each species according to its rarity and its rate of decline. This measure gives a better representation of field ecologists' intuitive valuation of the vegetation, and besides it is more sensitive to environmental changes than traditional biodiversity measures like the Simpson index (Huston 1994). We also used the number of species as a measure because of its attractive simplicity.

A very simple way to relate vegetation changes to the environment is the inspection of ordination diagrams. The consecutive observations at permanent plots can be summarised as mean 'sample scores' resulting from DCA, and plotted in a single ordination diagram. This will immediately show whether the change in vegetation is e.g. linear or oscillatory. From CCA diagrams one can even get an idea of the causal environmental factor. If in the diagram the change in vegetation and the change of a certain abiotic factor are in the same direction, one might infer that this abiotic factor is causing the change (Van Dobben & De Bakker 1996). The diagram also enables one to compare the temporal change with the spatial variation, with respect to both their magnitude and their mutual relation. Interesting questions might be e.g. whether the temporal change is large compared to the spatial variation, or whether the plots are becoming more similar in the course of time. However, although providing a visually attractive summary, such graphical techniques are insufficient to unequivocally ascribe the variation or the change in the vegetation to any environmental factor. We therefore used both the sample scores from DCA, and the CCV and number of species as input for a detailed statistical analysis based on linear regression, in which we attempted to separate the effects of weather conditions and soil subsidence on the vegetation.

As an indicator for freshwater influence we used the phreatic level in spring (PLS, measured in m relative to soil surface level). For seawater influence we used the flooding frequency (FF, in year⁻¹) as a measure. We first determined the effects of these two indicators on the vegetation using CCA, to test the hypothesis that they are causal factors indeed. Next, we tested the hypothesis that PLS and FF are determined by both the elevation of the soil surface and the weather conditions. As measures for weather conditions we used the net precipitation (P_{net} , i.e. precipitation minus evaporation, in m.y⁻¹), and the flooding frequency at a fixed level of 2 meter above the reference level (Amsterdam Zero) (FF₂, in y⁻¹). Subsequently we modelled the vegetation at each point in both space and time as a linear combination of the following variables:

- the elevation of the soil surface at the start of the monitoring in 1986;
- the subsidence of the soil surface that occurred since the start of the monitoring;
- the weather conditions (expressed as P_{net} and FF₂) in the period directly preceding each observation;
- the soil chemistry (that was determined only once and considered constant over time).



To detect any influence of soil subsidence we considered the change in the state of the vegetation over time as a signal that consists of three components:

- an oscillatory component, due to fluctuations in net precipitation;
- an oscillatory component, due to fluctuations in sea level regime;
- a linear component, due to soil subsidence.

We used multiple regression to separate these signals, and to determine their statistical significance.

As the rate of soil subsidence was more or less constant over time, any linear change in the vegetation might be ascribed to soil subsidence in the above approach. However, the vegetation may also respond by other factors that were not included in our study, but have a temporal trend as well. Such factors might be climatic ones other than precipitation or sea level (e.g. temperature), or atmospheric deposition. We used an extra check to avoid the risk of erroneously ascribing any linear trend in the vegetation to soil subsidence. For this check we made the hypothesis that the change in elevation has its effect on the vegetation instantly, or with a time lag that is constant and not too large. If that is the case, the change in the vegetation due to a given amount of soil subsidence can be estimated on the basis of the spatial pattern of both vegetation and elevation. Or, to put it in more general terms, if there is no or a constant time lag in the effect of environmental variable X , the change in vegetation at a given site S_1 in response to an environmental change from state X_1 at t_1 to state X_2 at t_2 can be predicted as the difference in vegetation at t_1 when moving from site S_1 to another site S_2 where environmental state X_2 was present at t_1 (Van Dobben & Ter Braak 1998). We performed our check by back-predicting the rate of soil subsidence from the change in vegetation and the spatial patterns of vegetation and elevation, and comparing the back-predicted subsidence rate to the actual rate. If these were not significantly different we concluded that the observed change was probably due to soil subsidence. This procedure is analogous to the one used by Van Dobben & Ter Braak (1998) to detect the effect of changes in atmospheric pollutants on the vegetation.

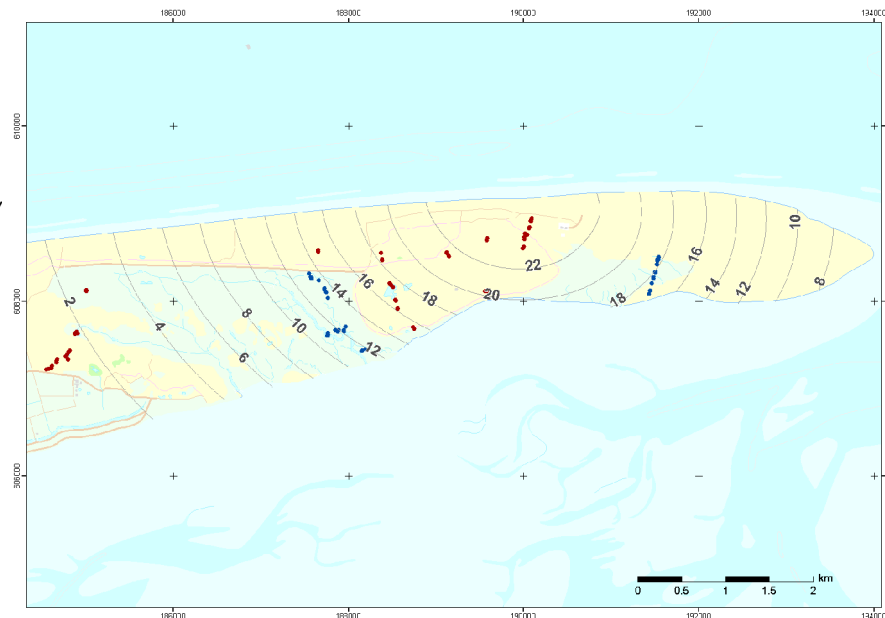


2. Material and methods

2.1. Vegetation data

Fifty-six permanent plots were laid out in 1986, before the start of the gas extraction, and 10 additional plots were laid out in 1989. All plots were 2x2 m² in size, and they were marked in the field using solid plastic posts with a height of c. 10 cm above the soil surface, that were placed 1 m outside the plot itself. The coordinates of the plots were determined, initially by standard geodetic techniques, and after 2000 by RTK-DGPS. The location of the plots, together with contour lines of soil subsidence, is shown in [figure 1](#). The plots were arranged in five transects, which cover a wide range of vegetation types in dry dunes, (periodical) freshwater pools, wet dune slack, and higher parts of the salt marsh. However, lower salt marshes, where soil subsidence is largely compensated by sedimentation (Dijkema et al. 2005), were outside the scope of this study. Besides covering a range of abiotic conditions, the plots also cover the whole range of subsidence values, from c. 25 cm in 2001 near the extraction point, down to c. 1 cm at 5 km away from the extraction point.

Figuur 1
Location of the plots, together with the total soil subsidence in 2001. Coordinates are in the national rectangular coordinate system. Red dots indicate plots treated by Van Dobben & Slim (this study), blue dots indicate plots by Dijkema et al. (2005).



The vegetation of the plots was sampled at three-yearly intervals, starting in 1986. Vegetation sampling was done by optically estimating the percentage cover per species; percentages were scored in a nine-point scale (described by Dirkse 1998) but back transformed before the statistical analysis. All bryophytes and lichens, and also vascular species that were not readily recognisable in the field, were collected for later identification. Only taxa that could be identified on the level of species were used in the statistical analysis, except *Taraxacum* sp. and *Callitriche* sp. *Rubus* species were taken together as *R. fruticosus*, except *R. caesius*. No subspecific taxa were distinguished except *Arenaria serpyllifolia* (subsp. *serpyllifolia* and *leptoclados*), *Eleocharis palustris* (subsp. *palustris* and *uniglumis*), *Galium palustre* (subsp. *palustre* and *elongatum*), *Galium verum* (subsp. *verum* and *maritimum*), *Lotus corniculatus* (subsp. *corniculatus* and *tenuifolius*), *Plantago major* (subsp. *major* and *pleiosperma*). Nomenclature follows Van der Meijden (1990), Touw & Rubers (1989), and Purvis et al. (1992) for vascular species, mosses and lichens, respectively. No distinction in layers (e.g. by using pseudo-species) was made.



A small number of missing values had to be estimated on the basis of observations in adjacent periods. This was the case for plot 406 in 1989 (assumed equal to 1986) and 1992 (assumed equal to 1995), and for plot 405 over the period 1989 - 1995. For the latter plot a linear trend in the cover of all species was assumed over the period 1986 - 1998. For the observations made in 1989 and 1992, the identifications of the bryophytes and lichens was considered unreliable because in these years no material was collected in the field. Therefore the cover percentage of these taxa was estimated from the observation in 1986 and 1995, again assuming a linear trend.

2.2. Abiotic data

The phreatic level was determined in piezometers that were installed in the autumn of 1986. One piezometer was installed for each group of 1-10 nearby plots (19 piezometers in total). These piezometers had a filter depth of c. 1.2 m. In the autumn of 1989 additional piezometers with a deeper filter (c. 1.5-2.0 m depending on local conditions) were installed adjacent to the ones already present. Water levels in these piezometers were recorded yearly on April, 26-28, and these levels are therefore further referred to as 'phreatic level in spring' (PLS). As the levels recorded in the deep-filter piezometers were only slightly different from those in the shallow-filter ones (difference 0-0.15 m, average absolute value 0.03 m) only the shallow-filter ones were used because these had the longest time series. In some cases data from the shallow-filter piezometers were not available (11A and 19A, removed after 1989; and 7A2, dry in 1992), and in that cases data from the deep-filter piezometers were used instead. [Table 1](#) gives the correspondence between the piezometers and the vegetation plots, together with their coordinates.

Table 1
Correspondence between plots and piezometers. Coordinates in m according to the Dutch National grid (see [figure 1](#)).

plot	X	Y	piezo-meter	plot	X	Y	piezo-meter
101	184554,4	607219,9	1A	419	188386,2	608467,1	19A *)
102	184580,9	607229,7	1A	419	188386,2	608467,1	19A-b *)
103	184610,2	607234,6	1A	420	188385,5	608478,8	19A *)
104	184618,0	607263,3	1A	420	188385,5	608478,8	19A-b *)
105	184669,8	607303,7	6A	421	188372,7	608552,7	21A
106	184670,5	607317,5	6A	606	189575,9	608117,4	7A2 *)
107	184675,3	607337,9	6A	606	189575,9	608117,4	7A-b2 *)
108	184801,5	607335,6	IV-A	607	189566,4	608117,7	7A2 *)
109	184800,0	607337,1	IV-A	607	189566,4	608117,7	7A-b2 *)
110	184775,7	607371,4	IV-A	608	189561,5	608117,8	7A2 *)
111	184793,9	607397,5	IV-A	608	189561,5	608117,8	7A-b2 *)
112	184807,0	607419,7	IV-A	609	189151,7	608514,8	10A
113	184809,5	607428,0	IV-A	610	189131,7	608543,6	10A
114	184818,2	607436,0	IV-A	611	189124,9	608554,0	10A
115	184877,1	607627,4	I	612	189119,6	608561,0	10A
116	184880,6	607631,4	I	613	189576,8	608693,8	14A
117	184886,4	607637,9	I	614	189581,2	608706,7	14A
118	184896,8	607650,3	I	615	189585,6	608719,7	14A
119	184900,9	607655,2	I	707	189988,1	608603,9	8A
120	184914,8	607634,6	I	708	189997,1	608613,2	8A
121	185012,7	608115,2	22A	709	190005,1	608621,3	8A
122	185011,6	608127,6	22A	710	190010,9	608710,8	11A
325	187659,3	608562,9	L550	710	190010,9	608710,8	11A-b *)
326	187658,9	608583,0	L550	711	190011,0	608737,7	11A *)
405	188748,1	607688,8	5A	711	190011,0	608737,7	11A-b *)
406	188735,8	607706,6	5A	712	190042,9	608758,8	11A *)
407	188563,1	607916,1	7A	712	190042,9	608758,8	11A-b *)
408	188559,3	607922,3	7A	713	190035,0	608762,3	11A *)
409	188544,2	608003,8	9A	713	190035,0	608762,3	11A-b *)
410	188541,7	608009,3	9A	714	190015,6	608772,4	11A *)
411	188540,0	608012,6	9A	714	190015,6	608772,4	11A-b *)
412	188538,2	608016,4	9A	715	190059,8	608834,1	17A2
413	188508,5	608158,9	17A	716	190059,3	608838,8	17A2
414	188496,9	608173,2	17A	717	190064,6	608845,5	17A2
415	188484,5	608187,3	17A	718	190084,0	608916,4	21A2



plot	X	Y	piezo-meter	plot	X	Y	piezo-meter
416	188481,9	608191,8	17A	719	190085,0	608920,0	21A2
417	188478,1	608196,5	17A	720	190088,0	608930,1	21A2
418	188469,0	608207,9	17A	721	190093,0	608947,7	21A2

*) deep-filter piezometer used, except in 1989 (value for 1986 estimated on the basis of 1991 - 1995)

As phreatic levels were not yet measured in spring 1986, these were estimated on the basis of the levels recorded on April 26-28 in the years 1989 - 1995, and the net precipitation during the preceding 6 month period (November - April). The water levels in each piezometer were regressed on net precipitation (rainfall minus evaporation), and the resulting regression equations (with an explained variance of c. 60-100%) were used to estimate the water levels in 1986 from the net precipitation over the period November 1985 - April 1986 (table 2).

Table 2
Regression of water levels in piezometers on net precipitation in the preceding 6 months. Fitted equation: groundwater level= $a_0+a_1(\text{net precipitation})$. Apr-86 is the water level estimated for April 1986, on the basis of the regression equation and the net precipitation in the preceding 6 months. Net precipitation and water level are in m.

piezometer	percentage explained variance	a0	a1	apr-86
1A	80%	1,028	-1,392	0,6851
6A	85%	1,164	-1,705	0,7449
IV-A	89%	0,834	-1,467	0,4727
I	52%	0,836	-1,974	0,35
22A	61%	0,643	-1,132	0,3643
L550	98%	0,867	-1,682	0,4538
5A	79%	0,582	-0,944	0,3495
7A	77%	1,379	-2,869	0,673
9A	67%	1,301	-2,42	0,7056
17A	67%	1,197	-2,323	0,6253
19A-b	85%	1,22	-1,898	0,7532
21A	90%	1,35	-2,23	0,8016
7A-b2	81%	1,513	-1,914	1,0426
10A	86%	0,664	-1,729	0,2386
14A	95%	1,153	-1,57	0,7665
8A	87%	0,507	-1,093	0,238
11A-b	100%	0,84	-1,597	0,4473
17A2	92%	0,897	-1,151	0,6137
21A2	94%	1,118	-1,288	0,8013

The **elevation** of all plots and all piezometers was determined relative to the Dutch standard reference level (Amsterdam Zero) by RTK-DGPS in 2001. Soil subsidence was described as a non-linear function of X and Y coordinate and time, that was parameterised on the basis of precision geodetic techniques and DGPS measurements carried out at regular intervals during the period 1985 - 2001 (Anonymous undated). The elevation of the plots over time was determined on the basis of the measured elevation in 2001 and the modelled soil subsidence. In doing so the assumption is made that no soil surface level changes take place due to other causes than gas extraction (e.g., sedimentation). This seems a reasonable assumption in view of the low flooding frequency of the plots (0-c. 0.5 day⁻¹, average 0.04 day⁻¹) and their distance to actively blown sand (c. 100 m). The water levels in the plots were calculated from the difference in elevation between the piezometers and the plots' soil surface in 2001, assuming (a) a horizontal phreatic plane, and (b) a difference in elevation between the piezometers and the plots that is constant over time. Also this assumption is reasonable because of the high porosity of the sandy soil and the short distance between the plots and the piezometers (c. 1-100 m, average 22 m).

Net precipitation was estimated from rainfall measured at a weather station in Nes (c. 10 km West of the study area), and evaporation at the nearest weather station where data were available (table 3). The vegetation in a



given year was related to precipitation minus evaporation summed over a period from November in the previous year up to April in that year.

Table 3
Weather stations where
evaporation data were
taken from.

year	station
1985	Ameland
1986	Ameland
1987	Ameland
1988	Terschelling
1989	Nes
1990	Terschelling
1991	Den Helder/Lauwersoog
1992	Lauwersoog
1993	Lauwersoog
1994	Lauwersoog
1995	Lauwersoog
1996	Lauwersoog
1997	Hoorn
1998	Lauwersoog
1999	Lauwersoog
2000	Lauwersoog
2001	Lauwersoog

Flooding frequency was calculated per calendar year for each plot. This was done on the basis of continuous sea level recording in the harbour at Nes, c. 10 km West of the study area, and the plot's elevation in each year. Some of the low-lying plots were inaccessible for seawater because they were located behind dunes, and therefore the accessibility for seawater was determined per plot, both directly from observations during a storm in 1998, and indirectly from measured Cl concentrations after a storm in 1990. A preliminary analysis of our data and other data (Eysink et al. 2000) showed a considerable lag in the vegetation's response to flooding. Therefore the vegetation in a given year was related to the mean flooding frequency of the two preceding years. The yearly variation in sea level regime was characterised by a variable denoted as FF_2 , which is the flooding frequency as determined above, at a level of 2 m above Amsterdam Zero (at this level flooding takes place c. 3 - 30 times per year).

Soil chemistry was determined in samples taken in 1995. Twenty-five coring with a diameter of 2 cm were taken to a depth of 25 cm at all sides, at a distance of c. 10 cm outside each plot. Humus was removed, and the samples were air dried and taken to the laboratory. Total N and P were determined colourimetrically after destruction with sulphuric-salicylic acid. Na, K and Ca were determined by AAS after destruction in Fleischmann acid. Chloride was determined by Chlor-O-Counter after water extraction at 20°. pH was determined potentiometrically in water extract.

2.3. Statistical methods

All abiotic data were checked for non-normality and outliers. Flooding frequency and all chemical data except pH were $(\ln(X-\min(X))+1)$ transformed to achieve normality. Cover percentages per species were $\ln(X+1)$ transformed. Other data were left untransformed.

The variability of the vegetation in space and time was explored by making a local classification using the program TWINSpan (Hill 1979). The plots were also identified according to the standard Dutch vegetation typology (Schaminée et al. 1998) using the program ASSOCIA (Van Tongeren in prep. cf. Wamelink et al. 2003). The relation between the local and the national typology was determined, but the local typology was used in the statistical treatment of the data. Detrended Correspondence Analysis (DCA), carried out by the ordination program CANOCO (Ter Braak & Smilauer 2002), was used to explore the mutual relations between the species and the



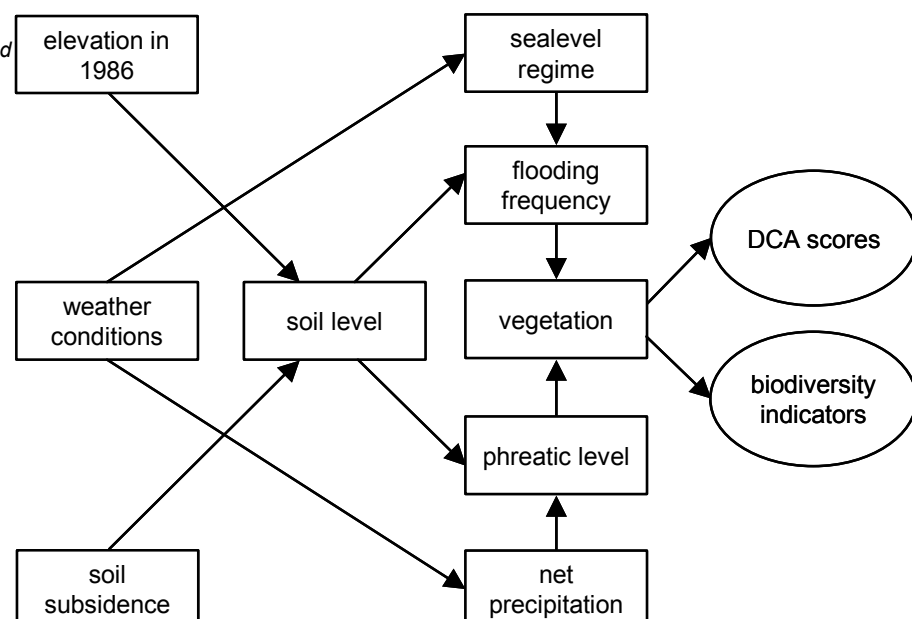
similarity of the plots; and its canonical form (CCA) was used to explore the effect of the abiotic variables and to make a ranking of their importance. Biplots resulting from DCA were used to visualize the temporal and spatial variation of the vegetation types.

The effect of soil subsidence was quantified using three descriptors for the state of the vegetation: (1) the 'sample scores' derived from DCA, (2) the 'Compound Conservancy Value' (CCV) and (3) the number of species. The CCV was computed according to Hertog & Rijken (1996) with a modification described in Sanders et al. (2004). A summary of the method is given by Wamelink et al. (2003). Essentially, this method assigns a value to each species proportional to its rarity and its rate of decline in The Netherlands, and adds the values per species to a value per plot. This value is expressed on an arbitrary scale which may be interpreted as follows: <12, vegetation with little conservancy value, probably consisting of few and common species; 12 - 16, vegetation which may have some conservancy value, rare or Red List species may occur; >16, vegetation with a high conservancy value, and a high probability for Red List species to occur.

Standard linear techniques (linear regression and REML; Robinson 1987) were used to relate the indicators for the state of the vegetation to the abiotic variables and their change over time. All computations were carried out by the program GENSTAT version 7.2 (Payne et al. 2003), except multivariate operations which were carried out by the program CANOCO version 4.5 (Ter Braak & Smilauer 2002).

The general model used to explain the temporal variation in the vegetation is depicted in figure 2. First, PLS and FF were modelled as an effect of weather conditions (i.e., net precipitation [P_{net}] and FF_2 , respectively) and elevation; and the vegetation descriptors were modelled as effects of PLS and FF. The soil subsidence was modelled as a linear function of time and distance to the gas extraction point. Next, it was attempted to model the vegetation descriptors directly as effects of weather conditions, elevation at the start of the gas extraction, and the subsidence that occurred since that moment. The resulting regression equations were used to back predict the soil subsidence, and the back predicted value was compared to the measured soil subsidence. If these two values corresponded, it was judged likely that the change in that vegetation descriptor was caused by soil subsidence. In a more formal way the method can be described as follows:

Figure 2
Conceptual model used
to evaluate the effects
of soil subsidence on
the vegetation.





the vegetation descriptor Y was modelled as a function of the abiotic conditions that directly influence it:

$$Y = a_0 + a_1X_1 + f(\text{time-independent variables}) + \text{error} \quad (1)$$

where Y : response variable (vegetation descriptor: DCA scores, CCV and number of species), X_1 : phreatic level or flooding frequency.

The abiotic variables X_1 that are under the influence of elevation (phreatic level and flooding frequency) were modelled as functions of elevation and weather conditions:

$$X_1 = b_0 + b_1Z + b_2X_2 \quad (2)$$

where X_1 : phreatic level or flooding frequency, Z : elevation, X_2 : net precipitation or flooding frequency at 2 m height.

Equations (1) and (2) can be combined into

$$Y = c_0 + c_1Z + c_3X_2 + f(\text{time-independent variables}) + \text{error} \quad (3)$$

where

$$c_0 = a_0 + a_1b_0$$

$$c_1 = a_1b_1$$

$$c_3 = a_1b_2$$

Next, the elevation of each plot was modelled as a linear function of its distance to the gas extraction point, and time. To do this, the soil subsidence area was assumed to be circular, and with a subsidence that linearly increases with time and with distance from the circumference of the circle. First, the radius of the circle was determined by extrapolation:

$$Z_t - Z_0 = d_0 + d_1D + \text{error} \quad (4)$$

where Z : elevation (0, in 1986; and t , in 2001), D : distance to the gas extraction point. From equation (4) it follows that

$$D_0 \approx -d_0 / d_1 \quad (5)$$

where D_0 : radius of the soil subsidence area.

Considering soil subsidence as linear in space and time, it follows that

$$Z_t = Z_0 + v(J - J_0)(D_0 - D) + \text{error} \quad (6)$$

where Z_t : elevation in year t (0, in 1986; 1, in 1987; etc), J : year ($J_0 = 1986$), D : distance to the gas extraction point ($D_0 =$ radius of the soil subsidence area), v : soil subsidence per year per meter distance from the edge of the soil subsidence area.

Now, equations (3) and (6) can be combined into

$$Y = c_0 + c_1Z_0 + c_1v(J - J_0)(D_0 - D) + c_3X_2 + f(\text{time-independent variables}) + \text{error} \quad (7)$$

In a multiple regression, c_1v can be estimated as the parameter c_2 of the term $(J - J_0)(D_0 - D)$. Therefore,

$$c_2 = c_1v \text{ or } v_{\text{est}} = c_2 / c_1 \quad (8)$$

where v_{est} : soil subsidence estimated on the basis of the vegetation change and the relation between vegetation and the elevation of the plot in 1986 (the 'back predicted' value).

Equations (6) and (8) yield independent estimates of v . If the change in Y over the years is caused by soil subsidence, these two estimates should have identical values. Therefore, the 99% confidence interval of v_{est} was determined by using Fieller's theorem (cf. Finney 1971 p. 78) and compared to the value of v from equation (6). If the value of v (the 'true' value) was within the 99% confidence interval of v_{est} it was considered likely that the change in Y described by the term for $(J - J_0)(D_0 - D)$ was due to soil subsidence.

The above method was applied twice, namely for $X_2 =$ net precipitation and for $X_2 =$ flooding frequency at 2 m. In the latter case that analysis was restricted to the plots that were accessible for seawater.



3. Results

3.1. Typology

The first three divisions of the TWINSPAN classification were used to make a local typology. The eight types resulting from this classification were reduced to six by merging three of the types in the dry dune vegetation that were judged too similar to justify a separate treatment. Global descriptions of the ecology of these type were derived from field observations. The local types have been assigned to alliances (and some of the plots to associations) following the identifications by ASSOCIA. In floristic and ecological terms the types can be described as follows:

type 1: Saginion maritimae; most plots are identified as Centaurio-Saginetum, Sagino maritimae-Cochlearietum danicae or Trifolio fragiferi-Agrostietum stoloniferae. Typical species: *Carex distans*, *Odontites verna*, *Linum catharticum*, *Plantago coronopus*. This vegetation type occurs in the sandy parts of saltmarsh and transitions between salt marsh and dunes.

type 2: Armerion, Lolio-Potentillion; mostly identified as Juncetum gerardi, Trifolio fragiferi-Agrostietum and Triglochino-Agrostietum. Typical species: *Juncus gerardii*, *Festuca rubra*, *Potentilla anserina*, *Eleocharis palustris* subsp. *uniglumis*. This vegetation type is widespread on the higher parts of the saltmarsh. Note that the lower saltmarsh is not included in this study (see Dijkema et al. 2005).

type 3: Nanocyperion flavescens, Hydrocotylo-Baldellion. The former alliance consists of annual species occurring on the shores of dune pools that are inundated during winter and dry during summer; e.g. *Lythrum portula*. The latter alliance consists of aquatic species e.g. *Ceratophyllum submersum*, *Polygonum amphibium*. But this type also contains many (semi-)aquatic species from other alliances e.g. *Litorella uniflora*, *Apium inundatum*, *Eleocharis palustris* subsp. *palustris*, etc. This type occurs in and on the shores of pools whose water level has a strong annual variation depending on precipitation.

type 4: Empetrium nigri, Caricion davallianae, Caricion nigrae, Nanocyperion flavescens. This type is quite heterogeneous from a syntaxonomic point of view, containing associations like Pyrolo-Salicetum, Junco baltici-Schoenetum, Cicendietum filiformis, Caricetum trinervi-nigrae, Caricion nigrae. Typical species are e.g. *Salix repens*, *Cirsium palustre*, *Calamagrostis canescens*, *Carex panicea*, *C. nigra*, *Rubus* spp., *Chamerion angustifolium*. This type usually consists of shrubs and more productive herbs, and occurs on eutrophicated parts of the gradient from saltmarsh to dune. There is often a noticeable influence of gulls or rabbits.

type 5: Nardo-Galion saxatilis, Empetrium nigri, Ericion tetralicis; associations most frequently found are Gentiano pneumonanthes-Nardetum, Pyrolo-Salicetum, and Empetro-Ericetum. This type represents the dune heath, with typical species like *Erica tetralix*, *Nardus stricta*, *Danthonia decumbens*, *Potentilla erecta*. It occurs on the oligotrophic but densely vegetated parts of the dunes.

type 6: Plantagini-Festucion, Polygalo-Koelerion, Empetrium nigri; association are e.g. Festuco-Galietum typicum, Polypodio-Empetretum, Salici repentis-Empetretum, Taraxaco-Galietum (fragarietosum and cladonietosum). Typical species: *Ammophila arenaria*, *Galium verum*, *Hypochaeris radicata*, *Hieracium umbellatum*, *Cladonia* spp. This type occurs on the oligotrophic, sandy and sparsely vegetated part of the dunes, often with a noticeable influence of rabbits.



Table 4 gives the type to which each plot belongs in the course of time. Most plots belong to a single type through the whole observation period, and if a plot changes its type this change is often only transient. The plots that did not belong to the same type all the time were assigned to the type to which they belonged most of the time, and this assignment was used in the further treatment of the data (**table 4**).

*Table 4
Assignment of plots to types in each year. The last column give the type assignment that was used in the statistical treatment of the data. See text for an explanation of the type numbers.*

plot	1986	1989	1992	1995	1998	2001	final assignment
101	3	3	3	3	3	3	3
102	6	6	6	6	6	6	6
103	5	5	5	5	5	5	5
104	6	6	6	6	6	6	6
105	6	6	5	5	5	6	6
106	5	5	5	5	5	5	5
107	6	6	6	6	6	6	6
108	3	3	3	3	3	3	3
109	3	3	3	3	3	3	3
110	3	3	3	3	3	3	3
111	4	4	4	3	4	3	4
112	4	4	4	4	5	4	4
113	5	5	5	5	5	5	5
114	5	5	5	5	5	5	5
115	5	5	5	5	5	5	5
116	2	4	2	2	2	2	2
117	2	2	2	3	2	2	2
118	3	2	2	2	3	2	2
119	3	3	2	3	3	2	3
120	3	2	3	3	3	3	3
121	2	2	2	2	2	2	2
122	4	4	1	1	4	1	4
325	4	4	4	4	4	4	4
326	4	4	4	4	4	4	4
405	4	4	4	4	4	4	4
406	6	6	6	6	6	6	6
407	4	4	4	4	4	4	4
408	5	5	5	5	5	5	5
409	4	4	4	3	4	4	4
410	3	3	4	3	4	3	3
411	3	3	3	3	3	3	3
412	3	3	3	3	3	3	3
413	3	3	3	3	3	3	3
414	3	3	3	3	3	3	3
415	3	3	3	3	3	3	3
416	3	3	3	3	3	3	3
417	4	3	4	3	4	3	4
418	6	6	6	6	6	6	6
419	4	4	4	4	4	4	4
420	4	4	4	3	4	4	4
421	4	4	4	4	4	4	4
606	-	5	5	5	5	5	5
607	-	6	6	5	5	5	5
608	-	6	6	6	6	6	6
609	-	6	6	6	6	6	6
610	-	4	4	4	4	4	4
611	-	4	4	4	4	4	4
612	-	4	4	4	4	4	4
613	-	4	4	4	4	4	4
614	-	4	2	2	4	2	2
615	-	5	5	4	4	4	4
707	4	4	2	2	2	2	2
708	2	2	2	2	2	2	2
709	2	2	2	2	2	2	2
710	1	2	2	2	2	2	2



plot	1986	1989	1992	1995	1998	2001	final assignment
711	2	2	2	2	2	2	2
712	1	2	2	2	2	2	2
713	2	2	2	2	2	2	2
714	1	1	1	1	1	1	1
715	1	1	1	1	1	1	1
716	1	1	1	1	1	1	1
717	1	1	1	2	2	2	2
718	1	1	1	1	1	1	1
719	1	1	1	1	1	1	1
720	1	1	1	2	2	2	2
721	1	1	1	2	1	1	1

3.2. Variation of the vegetation in space and time

Figure 3 is the biplot resulting from DCA, using the observations in all plots and at all points in time. The sample scores (**figures 3A** and **3C**) have been summarised as average values for each combination of type and observation year (note that for some of the types two points are plotted for 1989: one is the average of all plots, the other one is the average excluding the plots that were newly installed in 1989). The species plot (**figure 3B**) shows the arrangement of the species over the types, and is complementary to the type descriptions in 3.1. As an aid to the ecological interpretation of the plot, the relation with the 'Ellenberg' ecological indicator values (Ellenberg et al. 1991, Siebel 1993) per sample (plot / year combination) has been determined (**table 5**). The first axis mainly represents the gradient from salt marsh to dune (i.e. from salt, wet, neutral and nutrient rich to fresh, dry, acid and nutrient poor, which becomes apparent from its negative correlations with the Ellenberg scores for salinity, humidity, acidity and nutrients). The second axis mainly represents the gradient from saltwater influence to freshwater influence, which becomes apparent from its positive correlation with the Ellenberg scores for salinity and acidity. The third axis mainly represents a gradient from a low-productive (open) vegetation of nutrient-poor conditions to a high-productive (dense) vegetation of nutrient-rich conditions, which becomes apparent from its positive correlation with the Ellenberg score for nutrients, and its negative correlation with the score for light. These interpretations can be checked by comparing the ecology of the species (e.g. from Oberdorfer 1979, Weeda 1985-1994 or Van der Meijden 1990) with their positions in **figures 3B** and **3D**. The fourth axis has little correlation with the Ellenberg scores and neither is there an obvious interpretation for the species' positions on this axis, and it was therefore disregarded in subsequent analyses.



Figure 3A

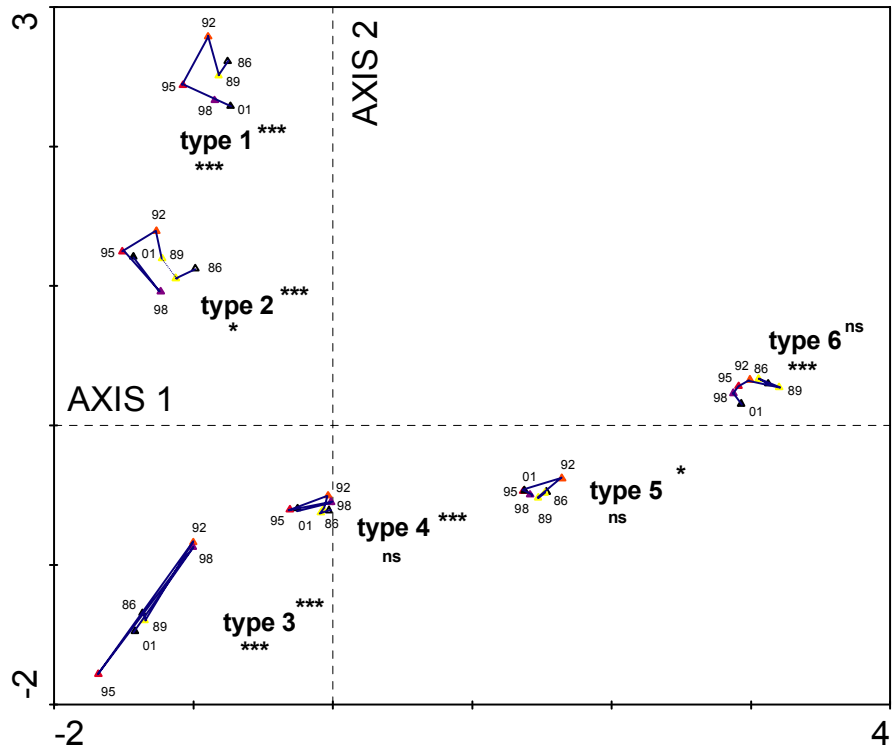


Figure 3B

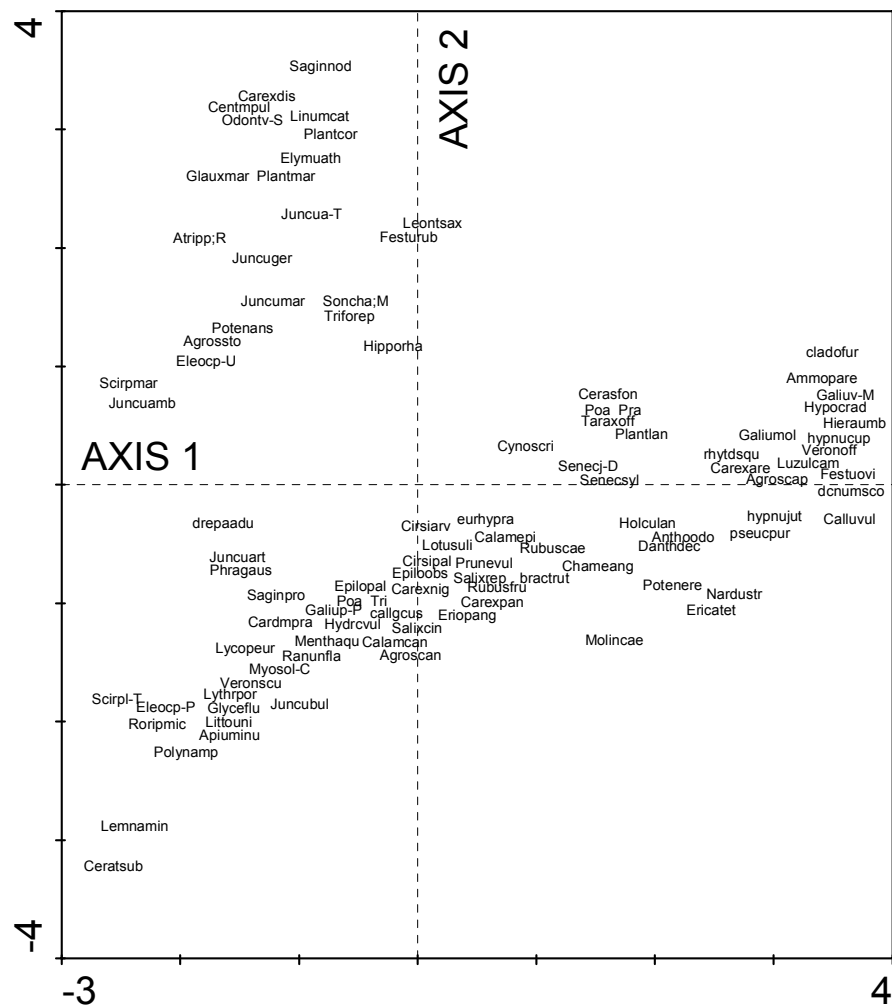




Figure 3C

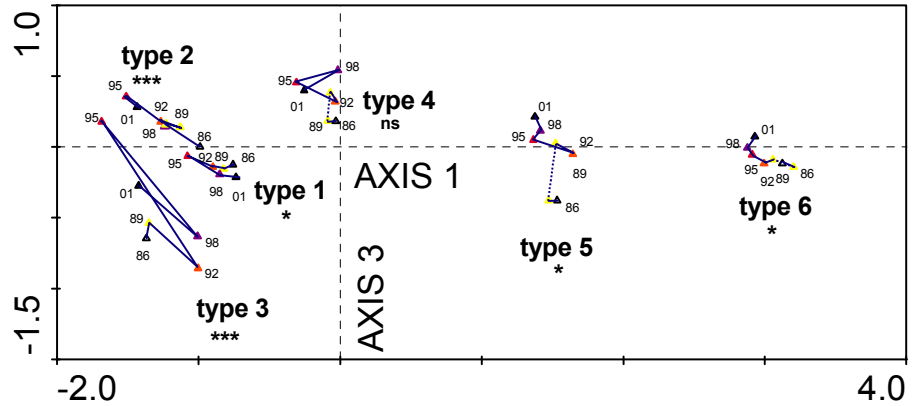


Figure 3D

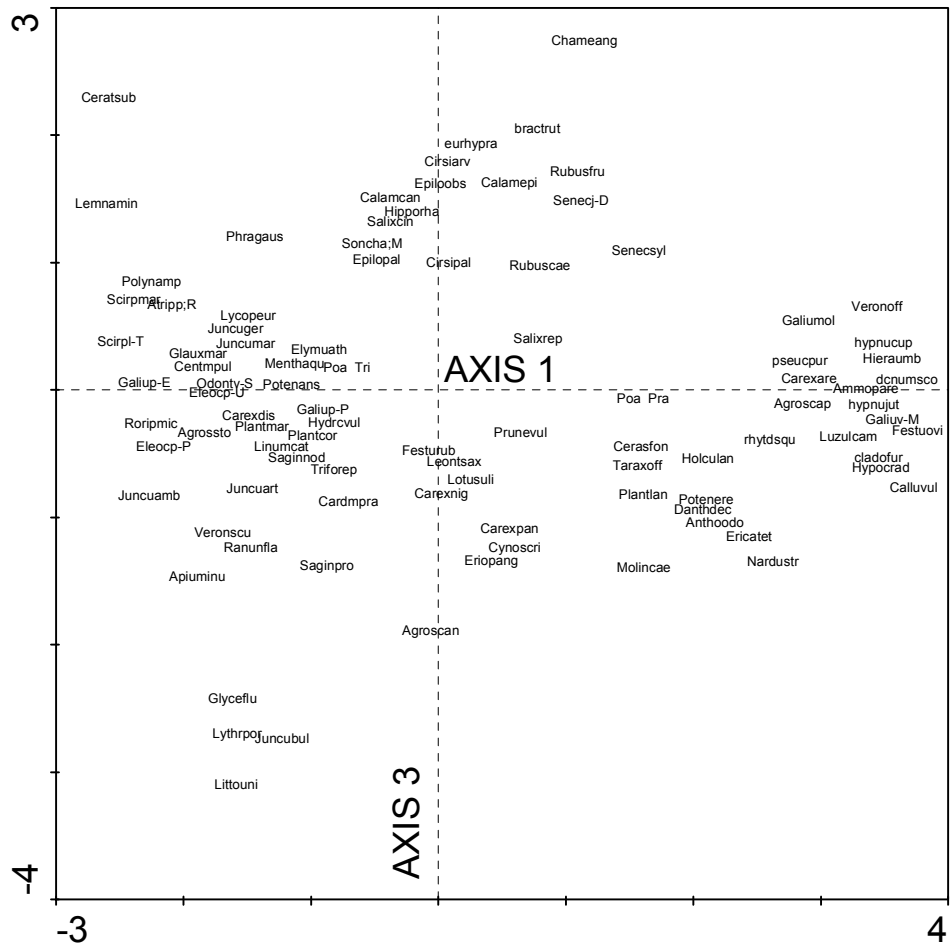


Figure 3

Biplot resulting from DCA using all plot / year combinations. Detrending by 2nd order polynomials, species cover logarithmized. Number of species: 276, number of samples: 386. Eigenvalues: $\lambda_1=0.708$, $\lambda_2=0.612$, $\lambda_3=0.457$, $\lambda_4=0.302$, sum of all eigenvalues = 12.750; the first three axes therefore represent 14% of the total variance in the species data. Species whose weight is less than 5% of the maximum species weight are not displayed.

A: axes 1 and 2, mean sample scores per plot / year combination, lines connect the values per type over time. The types where extra plots were installed in 1989 are displayed twice, with and without these extra plots, and connected by a dashed line. The significance of the temporal changes determined by REML is indicated to the right of each type number (for the first axis) and below each type number (for the second axis) (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, ns: $p > 0.05$. See table 8 for the significance of the linear trend.

B: axes 1 and 2, species.

C: axes 1 and 3, mean sample scores per plot / year combination. The significance of the temporal change on the third axis is indicated below each type number.

D: axes 1 and 3, species.

Explanation of abbreviated species names:

Agroscaan, *Agrostis canina*; Agroscaap, *Agrostis capillaris*; Agrossto, *Agrostis stolonifera*; Ammopare, *Ammophila arenaria*; Anthoodo, *Anthoxanthum odoratum*; Apiuminu, *Apium inundatum*; Atripp;R, *Atriplex prostrata* var. *prostrata*; bractrut, *Brachythecium rutabulum*;



Calamcan, *Calamagrostis canescens*; Calamepi, *Calamagrostis epigejos*; callgcsu, *Calliergonella cuspidata*; Calluvul, *Calluna vulgaris*; Cardmpra, *Cardamine pratensis*; Carexare, *Carex arenaria*; Carexdis, *Carex distans*; Carexnig, *Carex nigra*; Carexpan, *Carex panicea*; Centmpul, *Centaureum pulchellum*; Cerasfon, *Cerastium fontanum*; Ceratsub, *Ceratophyllum submersum*; Chameang, *Chamerion angustifolium*; Cirsiarv, *Cirsium arvense*; Cirsiipal, *Cirsium palustre*; cladofur, *Cladonia furcata*; Cynoscri, *Cynosurus cristatus*; Danthdec, *Danthonia decumbens*; dcnmsco, *Dicranum scoparium*; drepaadu, *Drepanocladus aduncus*; Eleocp-P, *Eleocharis palustris* subsp. *palustris*; Eleocp-U, *Eleocharis palustris* subsp. *uniglumis*; Elymuath, *Elymus athericus*; Epiloobs, *Epilobium obscurum*; Epilopal, *Epilobium palustre*; Ericatet, *Erica tetralix*; Eriopang, *Eriophorum angustifolium*; eurhypra, *Eurhynchium praelongum*; Festuovi, *Festuca ovina*; Festurub, *Festuca rubra*; Galiumol, *Galium mollugo*; Galiup-E, *Galium palustre* subsp. *elongatum*; Galiup-P, *Galium palustre* subsp. *palustre*; Galiuv-M, *Galium verum* subsp. *maritimum*; Glauxmar, *Glaux maritima*; Glyceflu, *Glyceria fluitans*; Hieraumb, *Hieracium umbellatum*; Hipporha, *Hippophae rhamnoides*; Holculan, *Holcus lanatus*; Hydrcvul, *Hydrocotyle vulgaris*; hypnucup, *Hypnum cupressiforme*; hypnujut, *Hypnum jutlandicum*; Hypocrad, *Hypochaeris radicata*; Juncuamb, *Juncus ambiguus*; Juncuart, *Juncus articulatus*; Juncua-T, *Juncus alpinoarticulatus* subsp. *atricapillus*; Juncubul, *Juncus bulbosus*; Juncuger, *Juncus gerardi*; Juncumar, *Juncus maritimus*; Lemnamin, *Lemna minor*; Leontosax, *Leontodon saxatilis*; Linumcat, *Linum catharticum*; Littouni, *Littorella uniflora*; Lotusuli, *Lotus uliginosus*; Luzulcam, *Luzula campestris*; Lycopeur, *Lycopus europaeus*; Lythrpor, *Lythrum portula*; Menthaqu, *Mentha aquatica*; Molincae, *Molinia caerulea*; Myosol-C, *Myosotis laxa* (subsp. *cespitosa*); Nardustr, *Nardus stricta*; Odontv-S, *Odontites verus* subsp. *serotinus*; Phragaus, *Phragmites australis*; Plantcor, *Plantago coronopus*; Plantlan, *Plantago lanceolata*; Plantmar, *Plantago maritima*; Poa pra, *Poa pratensis*; Poa tri, *Poa trivialis*; Polynamp, *Polygonum amphibium*; Potenans, *Potentilla anserina*; Potenere, *Potentilla erecta*; Prunevul, *Prunella vulgaris*; pseucpur, *Pseudoscleropodium purum*; Ranunfla, *Ranunculus flammula*; rhytdsqu, *Rhytidadelphus squarrosus*; Roripmic, *Rorippa microphylla*; Rubuscae, *Rubus caesius*; Rubusfru, *Rubus fruticosus*; Saginnod, *Sagina nodosa*; Saginpro, *Sagina procumbens*; Salixcin, *Salix cinerea*; Salixrep, *Salix repens*; Scirpl-T, *Scirpus lacustris* subsp. *tabernaemontani*; Scirpmar, *Scirpus maritimus*; Senecj-D, *Senecio jacobaea* subsp. *dunensis*; Senecsyl, *Senecio sylvaticus*; Soncha;M, *Sonchus arvensis* var. *maritimus*; Taraxoff, *Taraxacum officinale* s.l.; Triforep, *Trifolium repens*; Veronoff, *Veronica officinalis*; Veronscu, *Veronica scutellata*.

Table 5
Pearson correlation coefficients of the correlation between the sample scores on the first four axes and (unweighted) mean Ellenberg indicator values per plot.

	axis 1	axis 2	axis 3	axis 4
light	-0,37	0,51	-0,50	0,14
humidity	-0,82	-0,45	0,00	0,03
acidity	-0,65	0,57	0,30	0,00
nutrients	-0,57	0,23	0,51	0,05
salinity	-0,59	0,70	0,10	0,04
% expl. var (Ellenberg)	92,2%	88,5%	64,2%	3,0%
% expl. var (species)	5,6%	4,8%	3,6%	2,4%

% expl. var (Ellenberg) = percentage variance in the sample scores explained by the Ellenberg indicator values given;

% expl. var (species) = percentage variance in the species' abundance values explained by each axis ($=\lambda/\sum\lambda$).

In general, the sample plots show that the temporal change has been small compared to the spatial variation. Moreover there are no very clear temporal trends. The temporal variation seems to be oscillatory rather than monotonous, with the possible exception of the third axis where a general trend can be observed towards higher values in the course of time (figure 3C).

3.3. Effect of abiotic variables on the vegetation

The effect of the abiotic variables on the vegetation was explored by CCA and by linear regression. First, forward selection in CCA was used to determine the importance of the explanatory variables on the total species composition of the vegetation (Jongman et al. 1995). In each step of the selection process the term was added to the model that yielded the largest increase in fit, but subject to the constraint that its correlation with all terms already in the model should be lower than 0.6 in absolute value (table 6). The final CCA model contained terms for PLS, FF, N_{tot} , K, Ca and pH, and the effect of all these terms was significant as determined by the permutation test implemented in CANOCO ($p=0.001$ after 999 random permutations; details not shown). Figure 4 is the representation of the effect of the selected variables in the space of the biplot of figure 3 (note that the variable selection was done by CCA, but that the graphical representation



was done in DCA, so that figures 3 and 4 can be overlaid). Table 7 gives the result of a linear regression of the DCA scores on the first three axes, CCV and number of species, on the abiotic variables selected in CCA. The phreatic level and the flooding frequency have by far the strongest effect, and the effect of the soil chemistry is rather unimportant.

Figure 4A

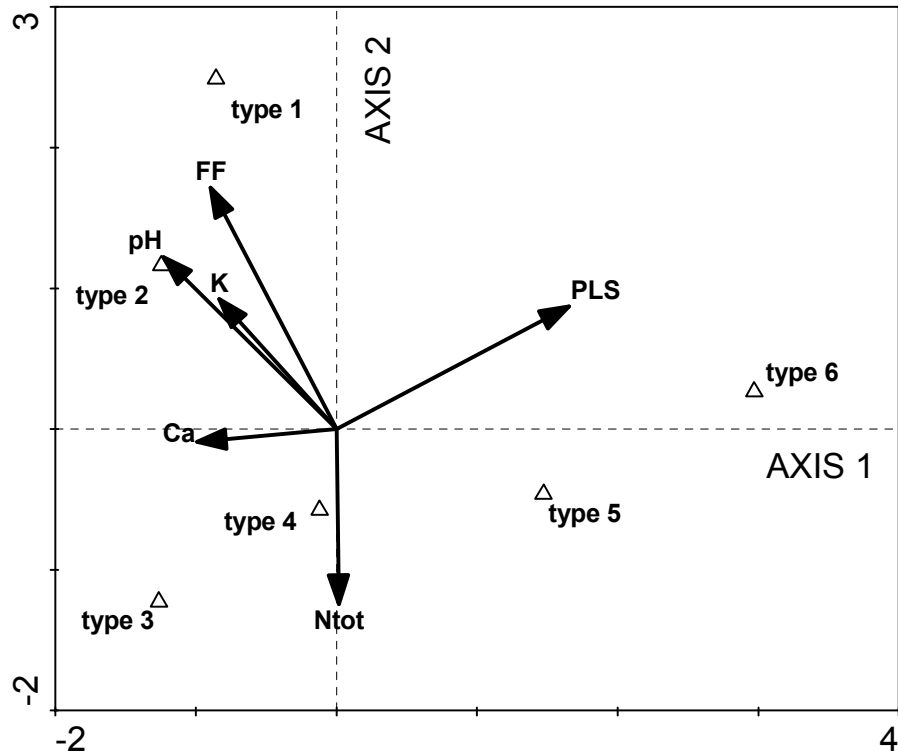


Figure 4B

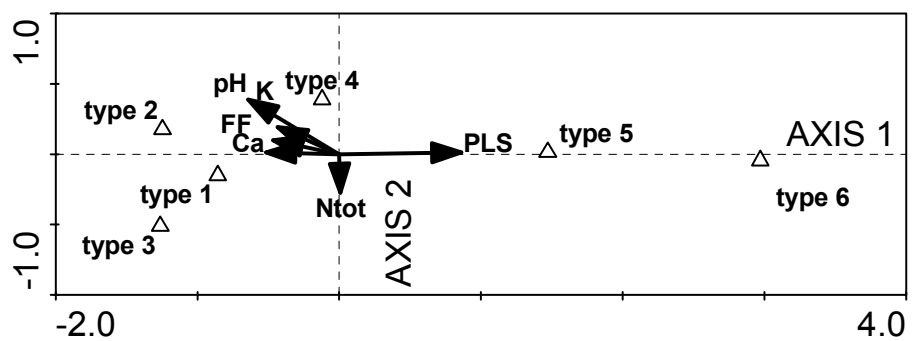


Figure 4

Correlation of environmental variables with sample scores depicted in figure 3. The coordinates of the heads of the arrows are the (scaled) correlation coefficients between the plot's scores on each axis, and the environmental variables. For the sake of comparison mean sample scores per type have been added. A: axis 1 and 2, B: axis 1 and 3.

Table 6
Correlation matrix of abiotic variables. PLS = phreatic level in spring, FF = flooding frequency, other symbols denote chemical contents in the soil.

	PLS	FF	Ntot	Ptot	Na	K	Ca	Cl
FF	-0,10							
Ntot	-0,24	-0,22						
Ptot	-0,26	-0,10	0,94					
Na	-0,15	0,39	0,53	0,62				
K	-0,18	0,35	0,55	0,66	0,91			
Ca	-0,33	-0,03	0,51	0,56	0,27	0,23		
Cl	-0,14	0,46	0,36	0,44	0,96	0,83	0,21	
pH	-0,25	0,51	-0,34	-0,17	0,22	0,17	0,28	0,27

Values >0.6 are in bold.



Table 7

Effect of the abiotic variables on the vegetation descriptors. The first row gives the total percentage variance explained by a model containing all terms, the other rows give the percentages variance uniquely due to each variable (i.e. the drop in percentage explained variance on omitting this term from the regression model), together with their regression coefficients and significance (***= $P < 0.001$, ** = $P < 0.01$, * = $p < 0.05$, ns = $p > 0.05$).

The regression coefficients for the axes can be interpreted as the expected displacement of the sample scores along each axis (in the scale given in figure 3) when an X-variable is increased or decreased by 1 unit (PLS, in m; FF, in $\ln(y^{-1})$, Ntot and K, in $\text{mg} \cdot 100\text{g}^{-1}$; Ca, in $\text{mg} \cdot \text{kg}^{-1}$). Note that these regression coefficients reflect the sum of the spatial and temporal variation, but are strongly dominated by the spatial variation.

	axis 1			axis 2			axis 3			CCV			N species		
	var. expl	regr. coef	P	var. expl	regr. coef	P	var. expl	regr. coef	P	var. expl	regr. coef	P	var. expl	regr. coef	P
all variables	81,8%			81,3%			21,6%			21,7%			20,6%		
PLS	27,9%	2,332	***	16,6%	1,466	***	0,0%	0,121	ns	0,0%	-0,036	ns	8,3%	6,768	***
FF	2,4%	-0,217	***	16,8%	0,468	***	8,4%	-0,246	***	2,7%	0,420	***	1,2%	-0,883	**
Ntot	0,0%	-0,022	ns	0,1%	-0,052	ns	0,0%	0,016	ns	0,9%	-0,375	*	0,1%	0,580	ns
K	0,0%	-0,017	ns	0,0%	0,056	ns	1,9%	0,220	**	3,3%	-0,828	***	1,2%	-1,585	**
Ca	0,2%	-0,089	*	0,9%	0,133	***	2,6%	-0,168	***	4,3%	0,619	***	4,7%	1,952	***
pH	0,9%	-0,396	***	0,1%	0,143	*	9,3%	0,737	***	0,0%	0,182	ns	0,3%	1,505	ns
undetermined	50,3%			46,7%			-0,7%			10,5%			4,6%		

3.4. Magnitude and significance of the temporal change

Both the close proximity of the sample scores per type in the various years (figure 3A) and the small number of type changes that occurred within a plot in the course of time (table 4), show that the temporal change is small compared to the spatial differences. To make sure whether any importance should be attached to the temporal changes, their statistical significance was determined in two ways. First, the presence of a temporal trend was detected using linear regression. In this analysis the effect of spatial variation was excluded by incorporating each plot as a dummy variable in the analysis (i.e. with value 1 for the records then belong to that plot, else 0), and the year number was used as an indicator for the temporal trend. Second, the significance of the temporal changes per se was detected by Residual Maximum Likelihood (REML). In this analysis each plots was used as a 'random' term and the observation year as the 'fixed' term. This technique was used because the unbalance introduced by the extra plots installed in 1989 prevents the use of the more simple ANOVA. The significance of the temporal change was determined by the Wald test (Engel 1990). Both analyses were carried out per type and for all types together, using the scores on the first three axes, the CCV and the number of species as the dependant variables.

Table 8 shows the significance of both the linear trend (as determined by a t-test of the regression coefficient of the year number), and the overall temporal effect (as determined by the Wald test). The latter significance levels are also indicated in figure 3. The overall temporal effect is significant ($p < 0.05$) for the first three axes and for the two biodiversity indicators, but a significant temporal trend is only present for the first axis (decreasing), the third axis (increasing) and the number of species (decreasing). If the sample scores per type are considered, the temporal variation is very small (and statistically significant in only one or two of the directions) for the types 4, 5 and 6. For the types 1, 2 and 3 this variation is larger (and significant in all directions), but often of an oscillatory nature (as shown by the nonsignificant linear trend).



Table 8
Significance of temporal effects.

Values are regression coefficients for year number (a_1) of the regression equation: vegetation descriptor = $a_{plot} + a_1 \cdot \text{year number}$. The first significance level pertains to a_1 , the second (in brackets) indicates the significance of the temporal effect determined by REML using the plots as the 'random' variables and the years as the 'fixed' variables (**= $P < 0.001$, ** = $P < 0.01$, * = $p < 0.05$, ns = $p > 0.05$). The regression coefficients can be interpreted as the yearly displacement of the sample scores along the axes, and the yearly change in biodiversity indicator values.

	axis 1		axis 1		axis 1	
all types	-0,011	*** (***)	-0,001	ns (***)	0,010	** (***)
type 1	-0,012	* (***)	-0,029	*** (***)	0,001	ns (*)
type 2	-0,029	*** (***)	0,009	ns (*)	0,022	*** (***)
type 3	0,009	ns (***)	0,009	ns (***)	0,016	ns (***)
type 4	-0,013	** (***)	-0,003	ns (ns)	0,000	ns (ns)
type 5	-0,011	* (*)	-0,002	ns (ns)	0,005	ns (*)
type 6	-0,012	* (ns)	-0,013	*** (***)	0,010	** (*)

	CCV		Nspec	
all types	-0,027	ns (*)	-0,144	*** (***)
type 1	0,013	ns (ns)	0,162	ns (ns)
type 2	-0,148	*** (**)	-0,435	*** (***)
type 3	0,044	ns (ns)	-0,105	ns (***)
type 4	-0,031	ns (ns)	-0,158	* (ns)
type 5	-0,005	ns (ns)	-0,017	ns (ns)
type 6	0,025	ns (ns)	-0,016	ns (ns)

Both biodiversity indicators have a downward trend that occurs in all types (table 8), however this trend is significant ($p < 0.05$) in a few cases only. By far the largest change occurred in type 2, where an expected (and statistically significant) loss of 6.5 species per plot occurred since the start of the observations (namely, 15 [the length of the observation period] times -0.435 [the regression coefficient for the number of species]). Also the decrease in CCV is significant in type 2. In type 3 there is a highly significant ($p < 0.001$) temporal effect on the number of species but no significant temporal trend. Apparently there were considerable fluctuations in the number of species in this type. Type 4 had a significant downward trend in the number of species, although the temporal effect itself was not significant (which may be due to the lower sensitivity of REML compared to linear regression).

Both the biodiversity indicators and the DCA scores are expressions of the floristic composition of the plots, and therefore there is a relation between these two measures. In figure 5 this relation is illustrated by projecting the gradients in biodiversity indicator values into the sample score plots of figures 3A and 3C. By combining these plots with figure 4 one might infer the expected change in biodiversity indicators on a given change in abiotic variables. For example, the arrow for FF (the flooding frequency) points in a upward direction in figure 4A. When flooding frequency increases in type 2, its sample score is expected to move in the direction of this arrow. In that case it would move into the direction of a higher CCV in figure 5A, and a lower number of species in figure 5C, so its CCV is expected to increase while its number of species is expected to decrease with increasing flooding frequency. Such inferences could also be made for other types and other abiotic variables. In the next paragraphs it will be attempted to quantify these relations.



Figure 5A

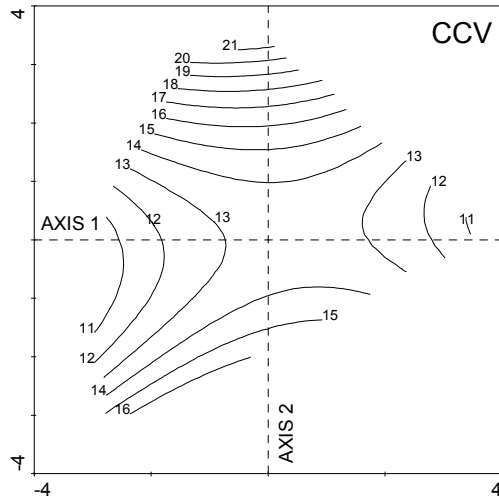


Figure 5B

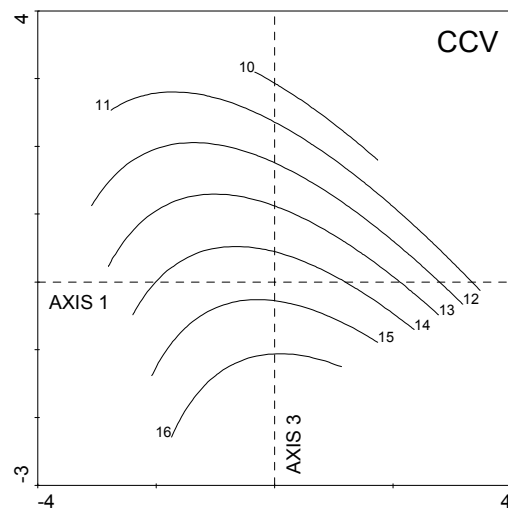


Figure 5C

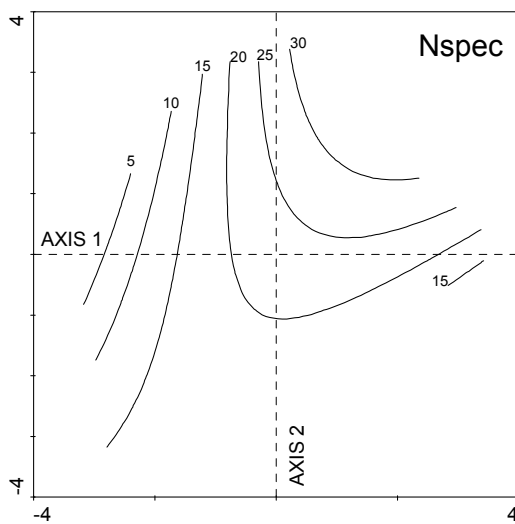




Figure 5D

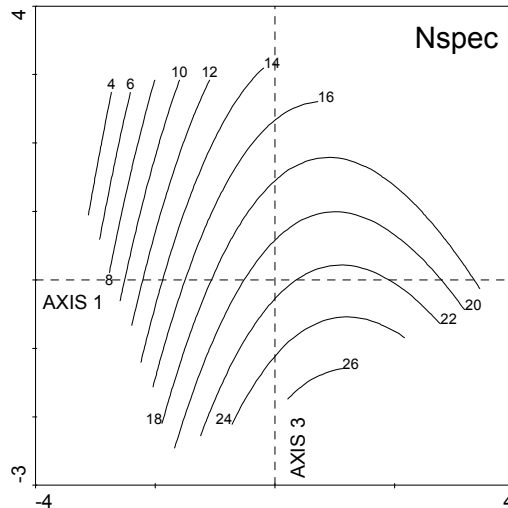


Figure 5

Gradients of biodiversity values projected into the plots of figure 3B and 3D. A: Conservancy value (CCV) relative to axes 1 and 2, B: CCV relative to axes 1 and 3, C: number of species (Nspec) relative to axes 1 and 2, D: number of species relative to axes 1 and 3. The isolines represent the fitted values of a second-order regression of the biodiversity indicators on the sample scores on both axes, and are restricted to the area where actual values occur. Interpretation of CCV: <12, low conservancy value; 12 - 16, intermediate conservancy value (rare or red list species may occur); >16, high conservancy value, high probability for Red List species to occur.

3.5. Relation between abiotic variables and weather conditions

To check the influence of weather conditions on the abiotic conditions that directly influence the vegetation, phreatic level in spring and flooding frequency were regressed on plot elevation, and the net precipitation and the flooding frequency at 2 m, respectively, following Equation (2). For both variables there were significant effects ($p < 0.01$) of both plot elevation and weather conditions (table 9).

Table 9

Parameter estimates of Equation (2), with phreatic level in spring (PLS) and flooding frequency (FF) as the Y variables, and soil level and weather conditions (as net precipitation Pnet or flooding frequency at 2 m FF₂) as the X variables. Significance levels: *** = $p < 0.001$, ** = $p < 0.01$. Units: PLS, Pnet and SL in m, FF and FF₂ in $\ln(y^{-1})$; note that the regression coefficients reflect the sum of the spatial and temporal variation, but are strongly dominated by the spatial variation.

	PLS		FF	
intercept	-0,722	***	7,377	***
SL	0,5165	***	-2,711	***
Pnet	-0,823	**	-	
FF ₂	-		0,2496	***

3.6. Relation between vegetation and weather conditions

Before exploring the combined effect of soil subsidence and weather conditions on the vegetation, the effect of the temporal fluctuation in the abiotic variables that directly influence the vegetation (phreatic level in spring and flooding frequency) was established. This was done by means of linear regression, in which the differences between the plots at the start of the observations were accounted for by including the plots themselves as a covariable; i.e. the regression equation that was fitted was:

$$Y = a_{\text{plot}} + a_1 X$$

where Y: vegetation descriptor, X: PLS or FF, a_{plot} : plot - dependent constant, a_1 : regression coefficient.



Table 10 gives the result of this regression analysis, which shows that most of the vegetation descriptors (except CCV) are indeed significantly influenced by the fluctuations in both phreatic level in spring and flooding frequency.

Table 10
Regression of vegetation descriptors ('Y variable') on phreatic level in spring (PLS) and flooding frequency (FF) ('X variable').

Model tested: $Y = a_{plot} + a_1X$
*Significance levels test whether a_1 is different from zero (***= $P < 0.001$, ** = $P < 0.01$, * = $p < 0.05$, ns = $p > 0.05$).*
Percentage explained variance are given for the full model ('X variable + plot'), and as the drop in explained variance on omitting the term for X from the model ('only X variable'). The plots that are inaccessible for seawater have been excluded from the determination of the effects of FF₂.
Note that AX-PLS and AX-FF have been scaled to make their variance equal to the variance of AX1 and AX2, respectively.

Y variable	X variable	perc. expl. variance		regression coefficient a_1	significance
		X variable + plot	only X variable		
AX1	PLS	98,0%	0,7%	0,948	***
AX2	PLS	94,7%	0,9%	0,887	***
AX3	PLS	88,5%	1,6%	-0,858	***
AX-PLS	PLS	97,2%	1,9%	1,541	***
AX-FF	PLS	95,8%	0,0%	0,135	ns
CCV	PLS	75,4%	0,0%	-0,100	ns
Nspec	PLS	76,3%	2,2%	8,906	***
AX1	FF	95,2%	1,4%	-0,294	***
AX2	FF	91,3%	0,2%	0,126	*
AX3	FF	79,7%	0,1%	0,069	ns
AX-PLS	FF	94,5%	0,5%	-0,191	***
AX-FF	FF	88,5%	2,6%	0,361	***
CCV	FF	73,2%	0,2%	-0,457	ns
Nspec	FF	68,3%	0,8%	-1,793	*

As set out in the Introduction, it was our aim to separate the effects of soil subsidence from the effects of variation in both net precipitation and sea level regime. Of the latter two variables the effect of net precipitation on the vegetation probably mainly comes about through the phreatic level as an intermediate variable. Similarly, the effect of sea level regime probably mainly comes about through the flooding frequency as an intermediate variable, although the phreatic level may also be relevant here. This means that in the DCA plot, the variation in the vegetation related to net precipitation will be in the same direction as the variation related to phreatic level, which has an angle of c. 30° with the first axis (figures 3A, 3B and 4A). Inspection of these figures also leads to the conclusion that the direction of variation in the vegetation related to sea level regime will be approximately perpendicular to the variation related to net precipitation, at an angle of c. 30° with the second axis. It may therefore be impossible to separate the effects of the two abiotic variables related to weather conditions on the basis of the scores on the DCA axes as established in figures 3 and 4, because the scores on both these axes are influenced by both abiotic variables.

In order to get a better separation of the effects of both weather-related variables, the axes were rotated such that the effect of each of these variables on the vegetation is represented as much as possible along a single axis. This was achieved by executing two extra CCA analyses, in each of which one of the two master variables (P_{net} and FF_2 , respectively) was used as the only explanatory variable. In such an analysis the first axis optimally represents the variation in the vegetation related to that single variable. These new axes are denoted AX-PLS (representing the effect of phreatic level) and AX-FF (representing the effect of flooding frequency). Table 10 shows that indeed the value of the regression coefficient for both variables is higher for the CCA axis that represents its effect compared to



both the original DCA axes, and to the new CCA axis that represents the effect of the other variable. The effect of PLS on AX-FF is even non-significant (note that scaling effects have been accounted for by making the variance of AX-PLS equal to that of AX1, and the variance of AX-FF equal to that of AX2). The effects of PLS and FF on the sample scores on AX-PLS and AX-FF are illustrated in [figures 6 and 7](#).

Figure 6
Temporal change of the mean value of phreatic level in spring (PLS) and the mean sample score on the axis optimised to represent the response of the vegetation to PLS (AX-PLS). For an easier comparison both variables have been standardized to zero mean and unit variance. The value for 1989 includes the extra plots installed in that year. Error bars indicate standard deviations (upper, of PLS; lower, of AX-PLS)

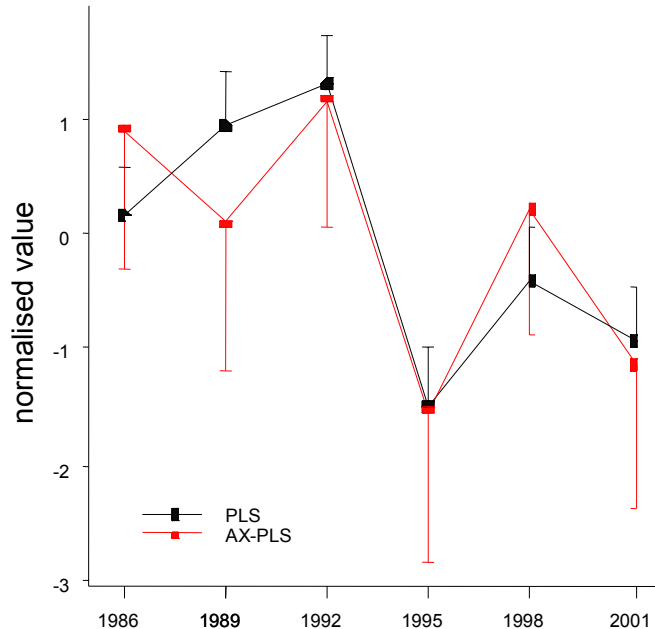
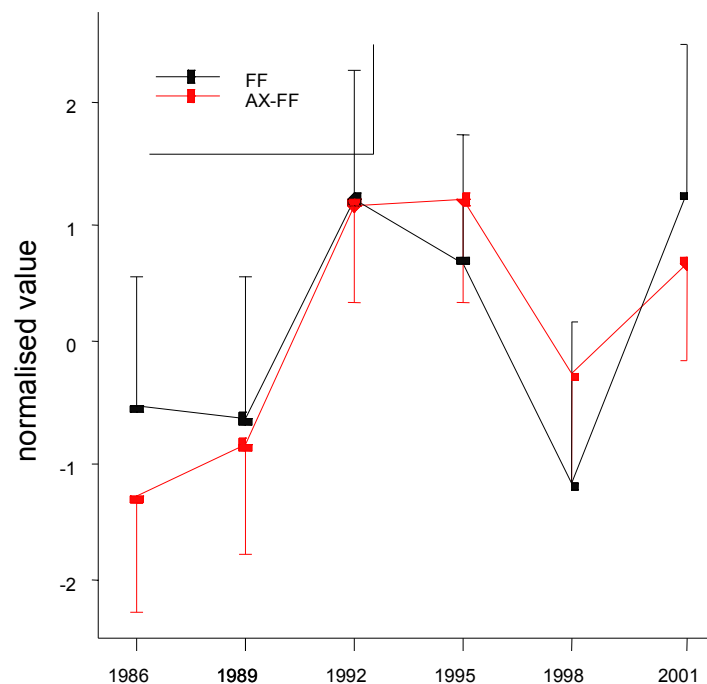


Figure 7
Temporal change of the mean value of FF and the mean sample score on the axis optimised to represent the response of the vegetation to FF (AX-FF), for the plots that are accessible for seawater. For an easier comparison both variables have been standardized to zero mean and unit variance. The value for 1989 includes the extra plots installed in that year. Error bars indicate standard deviations (upper, of FF; lower, of AX-FF).



An interesting comparison is between [table 7](#) and [table 10](#). [Table 7](#) gives the general effect of the abiotic variables (i.e., their combined spatial and temporal effect), and [table 10](#) gives their temporal effect only (the spatial effect being removed by including the plots themselves as covariables). However, the combined effect given by [table 7](#) is strongly dominated by the spatial variation as the temporal variation is far smaller (which for example becomes apparent from a comparison of the percentages explained variance



with and without including the spatial variation in [table 10](#)). A comparison of the magnitude of the spatial and temporal effects (through the regression coefficients in [table 7](#) and [10](#)) shows that these are in the same order of magnitude, or at least their signs are equal, but usually the temporal effect is smaller than the spatial effect. For example, the regression coefficient of axis 1 on phreatic level is 2.332 for the overall effect (which is strongly dominated by the spatial effect), and 0.948 for the temporal effect. Typically, the regression coefficient for the temporal effect has c. half the value of the regression coefficient for the overall effect. Only for the effect of flooding frequency on axis 1 the regression coefficient for temporal effect slightly exceeds the one for the overall effect. The situation for axis 3 is somewhat different because the overall effect of the phreatic level is not significant, but the temporal effect is highly significant; and for flooding frequency the reverse is true. For CCV there are no significant temporal effects while there is a significant overall effect of flooding frequency.

A smaller regression coefficient for the temporal effect compared to the overall effect can be explained from a lag in the response of the vegetation to abiotic changes. Or in other words: if abiotic conditions change from state X_1 to state X_2 , the vegetation starts to change in the direction of a vegetation occurring in a situation where X_2 has persisted over a longer period, however without becoming completely similar to the vegetation at X_2 within the three-year interval of our observations. Before this occurs, abiotic conditions again change in another direction, and the vegetation again follows this change with a certain lag.

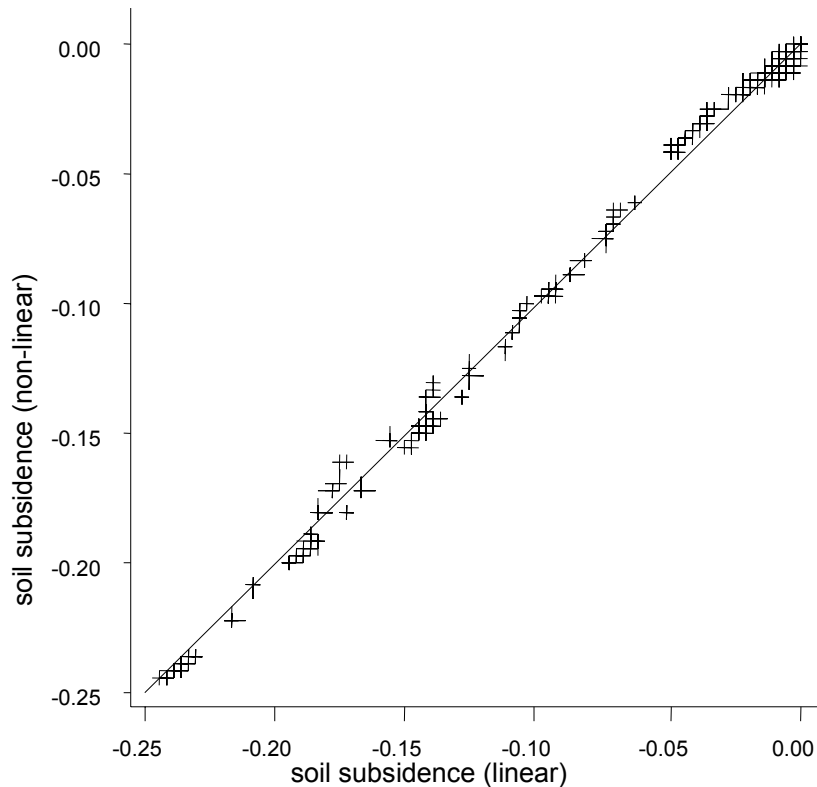
3.7 Effect of soil subsidence

In our approach we consider the vegetation descriptors as a function of three variables: (1) the spatial variation that was already present before the start of the gas extraction, (2) the weather conditions, and (3) the soil subsidence ([figure 2](#)). In principle, these can be separated by performing a multiple regression. As set out in the Introduction one should be aware that any linear (or at least, monotonous) change in the vegetation may result in a significant effect of the term for soil subsidence. We therefore performed an extra test on the magnitude of the regression coefficients before drawing conclusions on the effect of soil subsidence. The hypotheses behind this test is that the temporal change in any site due to a given amount of soil subsidence should be in the same order of magnitude as the spatial difference between two sites with a difference in elevation equal to that amount of soil subsidence (see Introduction). This principle is described in more formal terms in Eqs. (3), (6) and (7). Eq. (8) gives an opportunity to test the hypothesis that a linear change is due to soil subsidence indeed by back predicting the soil subsidence from the change in vegetation, and comparing the back predicted value to the real value.

In order to make the above back prediction, the soil subsidence has to be 'linearised', i.e. it has to be described as a linear function of space and time, so that only one parameter remains whose magnitude has to be checked. This was done by applying Eqs. (4), (5) and (6). A check was performed on the error of the linear model compared to the non-linear model described by Anonymous (undated). The linear and non-linear descriptions of the soil subsidence appear to be very similar ([figure 8](#)). In the following section, the error term in Eq. (6) was assumed to be zero, and the soil subsidence resulting from the linear model was assumed to represent the 'true' value.



Figure 8
Check of the 'linearised'
soil subsidence model.
Units: m. Regression
equation:
non-linear subsidence
in 2001 = $(1.000 \pm$
 $0.002) * \text{linear}$
subsidence in 2001
(99.7% explained
variance).
Drawn line is 1:1.



Next, the vegetation descriptors were modelled as a function of the elevation in 1986, the soil subsidence, and the weather conditions, following Eq. (7). The soil chemical variables whose effects were judged significant in the CCA analysis (i.e. the ones included in [table 7](#)) were used as 'time independent variables' (Eq. (7)). The contribution of soil subsidence and weather conditions to the explained variance was determined by omitting the terms for $(J-J_0)(D_0-D)$ and X_2 in turn, and by fitting the model with neither of these terms. The latter gives an estimate of the variance explained by the spatial pattern only (i.e., the soil chemistry and the elevation in 1986). The soil subsidence was back predicted on the basis of the regression coefficients estimated for the full model, and Eq. (8). The same procedure was also applied to phreatic level and flooding frequency, however without including the terms for soil chemistry, i.e. by replacing Eq. (3) by Eq. (2).

The result of the above analysis is given in [tables 11](#) and [12](#). When accounting for the effect of fluctuations in net precipitation there appear to be significant effects of soil subsidence on the sample scores on AX3, on AX-PLS (i.e. the first axis of a CCA using phreatic level as an explanatory variable), and on the conservancy value; and when accounting for the effect of fluctuations in sea level regime there appear to be significant effects of soil subsidence on the flooding frequency, and on the sample scores on AX1, on AX-PLS and on AX-FF (i.e. the first axis of a CCA using flooding frequency as an explanatory variable) ([table 11](#)).



Table 11
Effects of soil subsidence on phreatic level (PLS), flooding frequency (FF), CA and CCA axes, conservancy value (CCV) and number of species (Nspec), after accounting for effects of fluctuations in net precipitation (Pnet) and sea level regime (FF₂), following Eq. (7).

Explained variances relate to Eq. (7) ('full model'), Eq. (7) without the third term ('soil subsidence'), without the fourth term ('weather'), and without both these terms ('spatial pattern in 1986'). The absolute value of P is the significance of each regression coefficient in the full model (3: P<0.001, 2: P<0.01, 1: P<0.05, 0: P>0.05), the sign of P is the sign of the regression coefficient. The plots that are inaccessible for seawater have been excluded from the determination of the effects of FF₂.

Y variable	weather-related variable	full model		soil subsidence		weather		spatial pattern in 1986	
		var. expl.		var. expl.	P	var. expl.	P	var. expl.	P ¹⁾
PLS	Pnet	40,9		0,0	0	2,4	-3	38,5	3
AX1	Pnet	69,7		0,0	0	0,1	0	69,6	3
AX2	Pnet	45,3		0,1	0	0,0	0	45,3	2
AX3	Pnet	22,4		3,7	3	0,0	0	18,5	3
AX1-PLS	Pnet	58,9		1,4	-3	0,0	0	57,0	3
AX1-FF	Pnet	68,7		0,0	0	0,0	0	68,7	-3
CCV	Pnet	27,7		3,8	-3	0,8	1	24,1	-3
Nspec	Pnet	23,6		0,0	0	0,5	0	22,3	3
FF	FF ₂	95,4		7,0	3	6,5	3	84,7	-3
AX1	FF ₂	75,2		1,0	-2	0,2	0	74,3	3
AX2	FF ₂	61,3		0,0	0	0,2	0	61,4	0
AX3	FF ₂	39,5		1,1	0	0,0	0	38,8	-3
AX1-PLS	FF ₂	73,1		2,5	-3	0,0	0	70,7	3
AX1-FF	FF ₂	72,5		2,4	3	1,1	2	69,8	-3
CCV	FF ₂	43,8		1,0	0	0,0	0	43,0	1
Nspec	FF ₂	42,1		0,2	0	0,0	0	42,3	3

¹⁾ significance of the term for soil elevation.

In **table 12** the back predicted and the 'true' soil subsidence values are compared. This table should be read as follows: the values are the ratios between the back predicted and the 'true' values, and their 99% confidence limits. If 0 is within the range of the confidence limits for a given vegetation descriptor ('Y variable'), the effect of soil subsidence on that descriptor is not significant. If +1 is within this range, the change in this descriptor is consistent with its relation with elevation in 1986 and the measured soil subsidence. If the number in the column 'estimate' is above +1, the vegetation has changed more than expected on the basis of the measured soil subsidence; if it is between 0 and +1, the vegetation has changed less than expected on the basis of the measured soil subsidence. If the 'estimate' is negative, a rise in elevation has to be hypothesized to explain the observed vegetation change.

Table 12
Ratio of back predicted and 'true' soil subsidence. Back predicted values result from Equation (8), the 'true' value (-3.09523E-06 y⁻¹) from Equation (6). 'Lower' and 'upper' limit are the 99% confidence limits of the estimate determined according to Fieller's theorem. The plots that are inaccessible for seawater have been excluded from the determination of the effects of FF₂. * = no back prediction because the effect of elevation in 1986 is zero.

Y variable	weather-related variable	backpredicted / 'true' soil subsidence		
		lower limit	estimate	upper limit
PLS	Pnet	-1,78	-0,50	0,81
AX1	Pnet	-1,12	0,19	1,41
AX2	Pnet	-4,96	2,55	13,05
AX3	Pnet	-26,95	-7,63	-2,46
AX1-PLS	Pnet	0,68	2,12	3,61
AX1-FF	Pnet	-4,66	1,64	7,87
CCV	Pnet	-27,30	-7,93	-2,72
Nspec	Pnet	-1,88	0,77	3,16
FF	FF ₂	1,28	1,56	1,85
AX1	FF ₂	0,03	0,53	1,06
AX2	FF ₂	*	*	*
AX3	FF ₂	-0,56	1,62	5,57
AX1-PLS	FF ₂	0,32	0,93	1,59
AX1-FF	FF ₂	0,50	1,50	2,75
CCV	FF ₂	-0,98	2,66	277,12
Nspec	FF ₂	-0,60	0,52	1,72



Out of the variables with a significant effect, only AX-PLS (when accounting for the effect of either phreatic level or sea level), and AX1 and AX-FF (when accounting for the effect of sea level) yield back predictions of the soil subsidence that are within the expected range (i.e., +1 is within the range in [table 12](#), but 0 is outside this range). For phreatic level the effect of soil subsidence is not significant, but the back predicted soil subsidence is only slightly below the 'true' value. For flooding frequency the back predicted soil subsidence is only slightly above the 'true' value. However, large discrepancies are found for the effects of soil subsidence on the third axis and on the conservancy values. Here the ratio of the back predicted and the 'true' soil subsidence is negative, i.e. the elevation is expected to increase instead of to decrease. Apparently both these variables change over time, but the direction of this change is the opposite of the direction expected on the basis of their relation with the elevation in 1986 and the subsidence that occurred after that date. Therefore soil subsidence is not a satisfactory explanation for these changes. It can therefore be concluded that the trends in biodiversity (expressed as CCV or number of species) are either statistically not significant, or not attributable to soil subsidence. Inspection of [figure 5B](#) shows that a displacement of the sample scores in a positive direction on the third axis leads to a decrease in conservancy value, and therefore the two changes that are not attributable to soil subsidence may have the same cause.

[Table 13](#) gives the percentages variance in the fitted values that can be explained by soil subsidence, weather conditions, and the spatial pattern that is constant over time (these values are calculated for each term as the loss in explained variance on dropping these terms, relative to the explained variance of the full model). Of the vegetation descriptors a maximum of c. 3% of the variance in the fitted values is explained by soil subsidence, and a maximum of c. 2% is explained by weather conditions. For the abiotic conditions (PLS and FF) higher values were found, up to c. 7% for both weather conditions and soil subsidence. This analysis again shows that the changes in the vegetation over time have been small compared to the spatial differences. To be judged by the percentages explained variance, soil subsidence and fluctuating weather conditions have contributed to these changes in about equal amounts. However, as explained above, this approach will tend to over-estimate the importance of soil subsidence because it attributes any linear change to soil subsidence.

*Table 13
Percentage variance in the fitted values that can be explained by soil subsidence, weather conditions and spatial pattern, for those variables that yield a back predicted soil subsidence that is in the same order of magnitude as the 'true' value (irrespective of the significance of the effects).*

variable	weather represented by:	percentage variance in the fitted values that can be explained by:		
		soil subs	weather	spat pat
PLS	Pnet	0,0%	5,8%	94,2%
AX1	Pnet	0,0%	0,1%	99,8%
AX2	Pnet	0,1%	0,0%	100,0%
AX1-PLS	Pnet	2,4%	0,0%	96,8%
AX1-FF	Pnet	0,0%	0,0%	100,0%
Nspec	Pnet	0,0%	2,3%	94,5%
FF	FF ₂	7,3%	6,9%	88,8%
AX1	FF ₂	1,3%	0,2%	98,8%
AX3	FF ₂	2,7%	0,0%	98,3%
AX1-PLS	FF ₂	3,4%	0,0%	96,6%
AX1-FF	FF ₂	3,4%	1,5%	96,3%
CCV	FF ₂	2,3%	0,0%	98,0%
Nspec	FF ₂	0,4%	0,0%	100,0%



4. Discussion

Our analyses show that only small changes in the vegetation have occurred during the 15-year observation period. These changes are partly of an oscillatory nature, but some linear trends could also be detected. An important question is whether the changes can be interpreted as a loss of biodiversity. Our analyses show that there has been some loss of biodiversity, but in general this loss has been small. Both the CCV and the number of species have negative trends in nearly all types, but these trends are usually nonsignificant. The overall trend of the CCV is also nonsignificant. There is a significant overall decrease in the number of species, which is mainly due to the strong loss of species in type 2 (6 - 7 species per plot as an average over the whole observation period). A second important question is whether a loss of biodiversity (if there is any) is attributable to soil subsidence. In general this question has to be answered negatively. The effect of soil subsidence on the number of species is nonsignificant. There is a significant effect of soil subsidence on the CCV, however [table 12](#) shows that the actual change (a decrease in CCV) is the opposite of the change expected on the basis of its relation with elevation (an increase). It is therefore highly improbable that the loss of biodiversity is actually caused by soil subsidence.

Note that the expected change in biodiversity values resulting from soil subsidence cannot only be inferred from [table 12](#), but also by combining [figures 4](#) and [5](#). With soil subsidence, the flooding frequency is expected to increase, and therefore all sample scores are expected to move in the direction of the 'FF' arrow in [figure 4](#). In the case of type 2 in [figures 4A](#) and [5A](#), this would mean that the sample scores move in a direction where a higher CCV and also a slightly higher number of species is expected. On the other hand the displacement along the third axis would imply a slight decrease in CCV and number of species, but this displacement is expected to be small (because of the short length of the projection of the 'FF' arrow on the third axis). In general one should be aware that the above type of analysis is only an approximation because (a) it is based on expected values resulting from linear regression and not on the values themselves, and (b) only effects in the first two or three dimensions of an n-dimensional space are considered (n equals the number of species).

Despite the absence of a clear effect on biodiversity, soil subsidence did most probably cause some changes in the vegetation, but these changes cannot be interpreted as a loss of biodiversity. There is a significant effect of soil subsidence on the score on the first axis when accounting for the effect of flooding frequency; this effect is a shift towards lower values (compare the 'AX1 FF₂' row of [table 11](#); the regression coefficient in the 'soil subsidence' column is negative, and because this is the coefficient of the third term [$(J - J_0)(D_0 - D)$] of Eq. (7), this term will increase as with increasing soil subsidence). This effect is understandable on the basis of the relation of the axes with the environmental variables depicted in [figure 4A](#): the first axis is strongly positively correlated with PLS, and PLS is expected to decrease with soil subsidence (remember that a lower PLS means a higher groundwater level). No significant effects of soil subsidence on the second axis were found. This is not surprising as the sample scores on this axis did not have a significant temporal trend anyway ([table 8](#)).

Most difficult to interpret are the changes in CCV and in the sample score on the third axis, which have a significant relation with soil subsidence, but whose regression coefficients indicate that soil subsidence cannot be the causal factor. [Table 12](#) shows that these variables had a clear temporal trend which is the opposite of the temporal trends expected on the basis of their relation with the elevation of the soil at the start of the monitoring and



the subsidence that occurred over the observation period. For CCV, [tables 8](#) and [10](#) seem contradictory: [table 8](#) indicates no significant temporal trend, and [table 11](#) does indicate such a trend, at least when accounting for fluctuations in net precipitation. However, both tables are based on different regression equation which may have a different outcome (in [table 8](#), the plot itself is the covariable, and in [table 11](#) the weather conditions and the spatial pattern of soil elevation and chemistry). When the species plot ([figure 3D](#)) is inspected, the third axis seems to be positively correlated with the occurrence of highly productive species that are typical for nutrient rich conditions (e.g., *Chamerion angustifolium*, *Rubus* spp., *Cirsium* spp., *Calamagrostis canescens*). This is corroborated by the analysis of Ellenberg numbers ([table 5](#)), which indicates a strong decrease in light preference (i.e. a denser vegetation) and a strong increase in nutrient requirement towards higher values on the third axis. The measured abiotic variables do not have a very strong correlation with the third axis (cf. [table 7](#): 21.6% explained variance, compared to c. 81% for both the first and the second axis), with pH as the most important explanatory variable (9.3% explained variance).

It is tempting to ascribe the shift along the third axis to the general increase in nutrient availability that has been observed by many authors both in the Netherlands and adjacent countries (Veer 1997, Ketner-Oostra & Sýkora 2004, Jones et al. 2004, Provoost et al. 2004), which has resulted in an increase of productive species. The denser vegetation that resulted from this change has often out competed the rarer, less productive species, and has lead a general loss of conservancy value. This change, which has occurred over the past 2-3 decades, is usually ascribed to a combination of atmospheric deposition of nitrogen compounds, and a decreasing management intensity (e.g. by grazing). Also the recent collapse of the rabbit population might be a causal factor (Bijlsma 2004). In our data, both the loss of species, the decrease in conservancy value, and the shift of the sample scores toward higher values on the third axis, run surprisingly parallel ([figure 9](#)). Note that also [figures 5B](#) and [5D](#) indicate a negative relation between the third axis and the biodiversity indicators.

Figure 9

Temporal change of the mean values of conservancy value (CCV) (A) and number of species (Nspec) (B), plotted together with the mean sample score on the third axis. For an easier comparison all variables have been standardized to zero mean and unit variance, and the third axis has been inverted. Error bars indicate standard deviations (upper, CCV and Nspec; lower, AX3).

Figure 9A

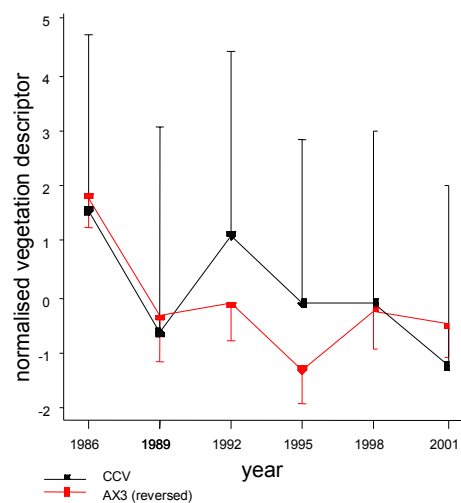
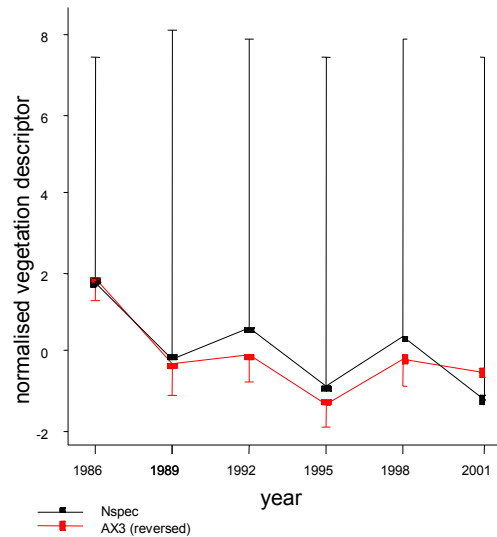




Figure 9B



Tables 10 and 11 show that there are also some significant effects of weather conditions. In contrast to effects of soil subsidence and the general trend towards eutrophication, which are monotonous trends, these effects are of an oscillatory nature. It can be inferred from table 8 that these effects are most prominent in type 3, where significant temporal effects occur in for all three axes and for the number of species, but where none of the vegetation descriptors has a significant trend. This is understandable on the basis of the ecology of this type, which consists of wet dune slack and shallow pools (vegetation types mostly belonging to the Nanocyperion). Here, the number of species and the CCV run strongly anti-parallel to the precipitation, with maximum values following dry periods in 1992 and 1998, and a minimum value following an extremely wet period in 2001 (data not shown). In this type the scores on all three axis also follow the above pattern (cf. figures 3A and 3C). An obvious explanation is that the water level in spring is a key factor. In dry periods this level is low, leaving a broad shore area for germination of annual species, while in wet periods these areas are under water and therefore less rich in species during the summer (During 1980).

Besides these rather prominent effects of fluctuations in fresh water influence, effects of fluctuations in flooding frequency can also be observed, e.g. by comparing figures 3A and 7. Both type 1 and type 2 reach their highest values with respect to the second axis in 1992, and in this year the flooding frequency was also high (although in 2001, when the flooding frequency was even slightly higher, the score of type 1 on the second axis was low). Also table 11 indicates some significant effects of flooding frequency.

In theory it would have been possible to detect the effects of precipitation, flooding frequency, and soil subsidence in a single analysis using multiple regression. This could be accomplished by e.g. incorporating two variables (namely, for net precipitation and flooding frequency) instead of the single X_2 in Eq. (7). However, there are two problems that prevent such an approach. First, the uncertainty in the estimates of the individual regression coefficients increases as more terms are included in the regression equation. As the effects of all explanatory variables used in our analysis are rather subtle, this would result in a loss of significance, so that ultimately no significant effects remain except the spatial pattern. And second, the flooding frequency cannot be linearly related to the soil subsidence because some of the plots are inaccessible for seawater anyway. This creates the necessity to include an extra term (namely, an indicator for the accessibility of each plot for seawater), which would aggravate the above problem still further.



On the basis of the above observations it can be tentatively concluded that (a) the temporal change in the vegetation is small, and is due to a combination of weather conditions, soil subsidence and eutrophication; and (b) these changes can partly be interpreted as a loss of biodiversity, but (c) this loss of biodiversity is due to eutrophication rather than to soil subsidence. However, one should be aware that the effect of weather conditions on the vegetation occurs with a certain time lag (cf. [Section 3.6](#)). It is therefore plausible that such a lag also occurs in the effect of soil subsidence. However, because the soil subsidence constitutes a linear trend that was present right from the start of the observations, it is not possible to detect such a lag at this moment. Therefore the changes due to soil subsidence might continue for some time after the termination of the gas extraction, and its final effect might be larger than inferred on the basis of the present data.



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