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The effect of fluctuations in tidal inundation frequency on a salt-marsh vegetation

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Abstract

Over a period of 15 years recordings were made of the species cover in permanent plots on the salt marsh of one of the West Frisian Islands, Schiermonnikoog (The Netherlands). Correlations between annual changes in the cover of the major species, and fluctuations in the monthly frequency of inundation by seawater were studied. First, a spectral analysis was carried out on the inundation frequency data to look for predictable patterns. Subsequently, fluctuations were defined as deviations from these predictable patterns. In a repeated multiple regression model, the effects of the season in which the fluctuations occurred, and the elevational position of the plots on the salt marsh were studied as factors influencing the correlation patterns. The behaviour of various species is discussed in relation to their seed bank characteristics and their salt tolerance.

Nomenclature: follows Heukels, H. & van der Meijden, R. 1983. Flora van Nederland. Groningen.

Introduction

Vegetation composition is variable in time and the perception of change varies with the scale at which vegetation is regarded. Succession is a directional change away from an initial stage, whereas fluctuations can be defined as reversible changes about a notional mean (Miles 1979). The latter are the subject of this study.

Many examples of supposed relationships between fluctuations in vegetation and variation in the abiotic environment (such as temperature, precipitation and high tide level) are known from the literature. Korchagin & Karpov (1970) found that periods of extreme cold in winter in the boreal taiga can kill large numbers of normally frost-resistent trees. Watt (1978) reported that after severe frost the cover of *Holcus lanatus* was reduced in temperate pastures. Beeftink *et al.* (1978) mentioned the dying-off of *Halimione portulacoides* in temperate salt marshes after extreme winters. Rosén (1985) described death and subsequent recovery of *Calluna vulgaris* on a limestone grassland after severe drought.

Fluctuations in rainfall have major effects on vegetation. Over a period of 30 yr the floristic composition of prairie grasslands fluctuated strongly as a result of recurring droughts (Coupland 1974). Recordings over a 10 yr period showed year-to-year differences in the amount of precipitation which caused fluctuations in the proportion of species present in a temperate flood-meadow (Rabotnov 1966). The coverage of *Holcus lanatus* in a temperate river-valley grassland declined temporally in both very dry years and in years with a very wet spring over a ten-year period (Bakker & de Vries 1985). Fluctuations in the cover percentages of species in temperate wet grasslands (over 3 yr), in chalk grasslands (over 8 yr) and in dune grasslands (over 3 yr) have also been related to variation in the amount of precipitation by Fliervoet (1984), Dierschke (1985) and van der Maarel (1981), respectively. Van Tooren *et al.* (1983) found a relation between specific life-history characteristics of some beach plain species and their reaction to fluctuations in the environmental circumstances over 8 yr.

The mean deviation of the high tide level and yearly amplitude, caused by storms, shows an irregular pattern with a tendency to clustering in deviations from the normal 18-year nodal cycle (Beeftink 1987). These clustered yearly deviations can cause fluctuations in the cover of salt-marsh species (Beeftink 1987; Cramer & Hytteborn 1987).

All those authors suggested the existence of a correlation between fluctuations in the composition of the vegetation and the occurrence of deviations from average abiotic conditions without quantifying the relationships through statistical analysis.

In this study the temporal pattern of the tidal fluctuations will first be analyzed in a spectral analysis to look for any predictable patterns. After this, the year-to-year fluctuations in plant populations on an abandoned salt marsh will be correlated in a multiple regression analysis with the number of inundations of the permanent plots per period of three months (corrected for predictable patterns). Beeftink (1987) found that the reaction of *Aster tripolium* to changes in inundation frequency depended on the elevation of the plots. In order to account for such possible interactions between temporal and spatial variation, the correlation analysis is repeated for plots on different elevation levels on the salt marsh.

Material and methods

Study area

The study area is located on the Oosterkwelder salt marsh on the island of Schiermonnikoog, which is one of the Dutch Frisian islands (50°30′N, 6°10′E). After a long period of grazing the salt marsh was abandoned in 1958. The study period started in 1971 and ended in 1985. Several plant communities were found in the study area, and they were dominated by *Puccinellia maritima* or *Halimione portulacoides* in the lower part, while in the mid- and upper part of the salt marsh *Juncus gerardii, Juncus maritimus, Festuca rubra, Artemisia maritima* and *Elymus pycnanthus* were the most frequently occurring species. Figure 1 shows the elevational position on the salt marsh of some of the species used in the present study (after Bakker *et al.* 1985). These data were

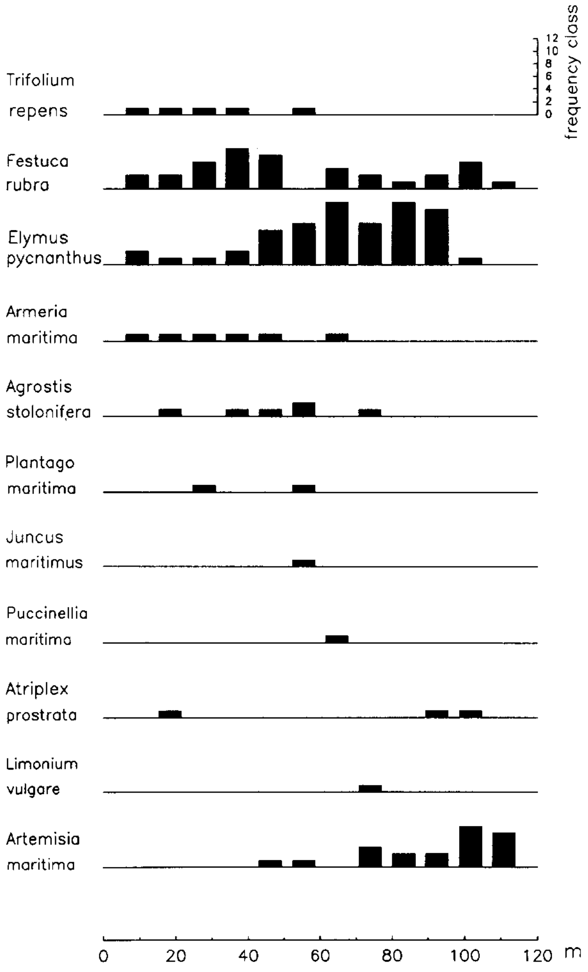

Fig. 1. Occurrence of species recorded in August 1984 in the abandoned area in 10 m sections along an elevational gradient. Frequency classes were obtained from point quadrat analysis: class 1 = 1 to 9 hits, class 2 = 10 to 19 hits etc. The gradient declined between 1.5 and 2.5 m. +N.A.P. (after Bakker *et al.* 1985).

recorded on the same elevational gradient used in this study.

Different successional patterns can be distinguished in this area, e.g., an increase in the *Halimione portulacoides* community on the lower salt marsh and an increase of *Elymus pycnanthus* on the mid- and upper salt marsh (see Bakker 1978; Bakker & Ruyter 1981; Bakker 1985; Bakker *et al.* 1985). The plots used in this study are situated in the mid salt-marsh vegetation.

Table 1. Arrangement of permanent plots into subsets, with the corresponding elevation of the salt marsh.

Elevation class	Elevation (cm +N.A.P.)	Plot number
1	100 – 120	22, 25, 26
2	121 – 140	19, 27
3	141 – 160	34
4	161 – 180	13, 32, 33, 35, 43, 48
5	181 – 200	5, 7, 8
6	201 – 220	1, 36, 40, 42, 47

Field methods and statistical analysis

The percentage of cover of all the occurring species was estimated annually in 20 permanent plots of 4 m^2 (Table 1). A decimal scale (Londo 1976) was used for the estimation. The correlations were only computed for species which covered over 10% in at least one plot in a year. Fourteen species remained after this selection (see Table 2). The year-to-year changes in cover of the species in each plot were computed and used as the dependent variables. This change was only computed when a species covered over 5% in both years.

The elevation of the permanent plots on the salt marsh in cm +N.A.P. (Dutch Ordnance Level) was determined relative to a reference point. The plots were arranged into six subsets occurring in different elevation classes (Table 1). In the regression analysis, no further distinctions were made between the plots within each subset. Data on the monthly inundation frequency of each elevation class were obtained from the Dutch Coastal Engineering Service (Rijkswaterstaat). They were recorded at a point 1 km away from the study area along the Wadden-coast of the island.

Table 2. The partial regression-coefficients added together over all seasons, and summed for the first three and the second three elevation classes. These sums are given separately for the positive and the negative coefficients. For each species the type is given: L = low salt-marsh species, M = middle salt-marsh species, D = dune species, with intermediates. ns., multiple regression not significant; –, species not abundant enough for regression computation (see text).

Species	Elevation (cm + N.A.P.)				
	100 – 160		161 – 200		
	Pos. corr.	Neg. corr.	Pos. corr.	Neg. corr.	Type
Triglochin maritima	-	-	5.80	n.s.	L
Limonium vulgare	0.35	– 0.37	n.s.	n.s.	L
Halimione portulacoides	n.s.	– 4.84	n.s.	n.s.	L
Puccinellia maritima	n.s.	– 4.84	1.85	– 4.16	L
Juncus gerardii	–	–	32.51	– 4.85	L/M
Festuca rubra	3.44	– 4.19	11.67	– 3.98	M
Juncus maritimus	–	–	2.81	n.s.	M
Artemisia maritima	n.s.	n.s.	1.32	– 2.18	M
Armeria maritima	n.s.	– 1.33	n.s.	n.s.	M
Plantago maritima	n.s.	– 1.14	n.s.	n.s.	M
Agrostis stolonifera	0.51	– 1.62	n.s.	n.s.	M
Atriplex prostrata	–	–	n.s.	– 6.63	M
Elymus pycnanthus	n.s.	n.s.	n.s.	n.s.	M/D
Trifolium repens	n.s.	n.s.	n.s.	n.s.	M/D

These data showed both strong random fluctuations and a repeated seasonal pattern (see Fig. 2 for an example). A spectral analysis was performed to determine the relative importance of possible repeated patterns, using the program 1T from BMDP (Dixon 1983). The underlying concept of spectral analysis is that each variable, thought of as a time series or function over time, can be represented by pure sine waves summed over different frequencies, with different amplitude and phase at each frequency. The spectral density function gives the distribution of the variance of the data over different frequency bands. It proceeds by Fourier transforming the data to obtain the coefficients of the sinusoids at a discrete set of frequencies. Neighbouring frequencies are grouped into frequency bands, and various quantities from the Fourier transformed data are estimated in one frequency band at a time (Dixon 1983). The log spectrum showed a clear maximum at the frequency of 0.083 cycles/month (that is 1 cycle/yr, Fig. 3). This means that most of the cyclic variation in the data can be ascribed to a one year cycle. Only the results of the elevation class 1 are given, because all the other classes had similar patterns.

Since we were interested in the effect of deviations in the inundation frequency from the normal patterns, the effect of this one-year cycle had to be separated from the random fluctuations. To do this the average January frequency (over 15 yr) was subtracted from each individual January frequency, and this was repeated for each month of the year. Subsequently, the mean of the entire time series was added to each corrected frequency. This was done for all six elevation classes. These corrected monthly frequencies were added together in three-month periods for each year for each elevation class: winter (December to February), spring (March to May), summer (June to August) and autumn (September to November). In this way, a corrected frequency was obtained which was independent from the normal seasonal pattern. All the remaining variations in the data were therefore considered to be fluctuations. From now on, the term inundation frequency will refer to these corrected values.

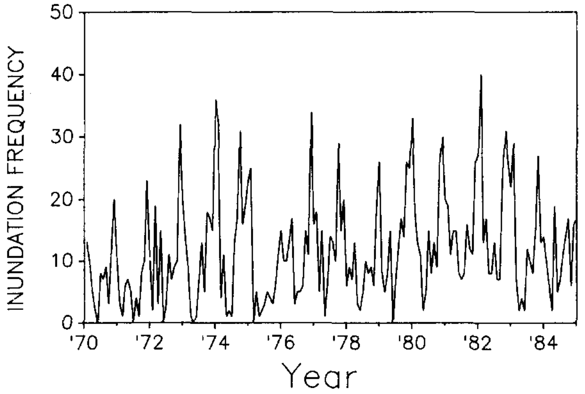

Fig. 2. The monthly transgression frequency of 100 cm +N.A.P. (Dutch Ordnance Level) on the island of Schiermonnikoog from January 1, 1971 to December 31, 1985. (Data from Rijkswaterstaat.)

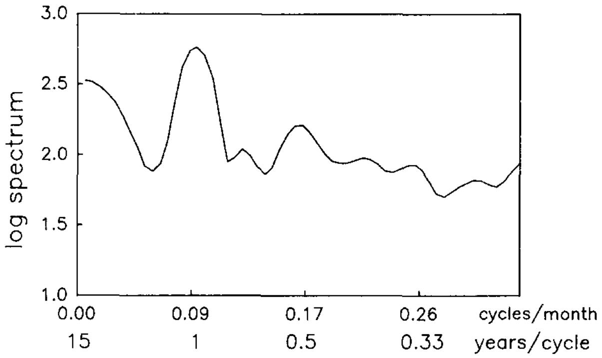

Fig. 3. The relative contribution (log spectrum) of each period length to the total variability of the transgression frequencies in Fig. 2 (see text).

The correlation between the change of cover of each species (dependent variable) and the corrected inundation frequencies in 8 preceding three-month periods (8 independent variables) was computed in a stepwise multiple regression analysis. The aim of this analysis was to determine in which periods the inundation frequencies were statistically related to the change in cover of each species, and in what order of importance. Stepwise multiple regression corrects for correlations between the independent variables. The partial regression coefficients are an indication of the direction and magnitude of the effect. Another variable is entered into the model only if it explains a part of the variance in the dependent variable that has not already been explained by other independent variables in the model. The variables were entered into the model according to the criterion of the highest F-value. The mimimum acceptable F to enter a variable was 4.00 and variables in the model having an F-value lower than 3.9 were removed.

Results

The change in cover of some main species in several plots is presented in Fig. 4. None of the species shows a clear successional trend; all changes seem to be reversible, and are therefore considered to be fluctuations. Furthermore, from this figure it can be concluded that, within a given elevation class, the pattern of changes of a species is more or less similar in different plots. This indicates that a common cause is involved.

The multiple regression between the corrected inundation frequency and the change in cover over a year was significant in 12 out of the 14 species. Both positive and negative partial regression coefficients were found. A positive coefficient means that with more inundations the cover of the species increased more, or decreased less.

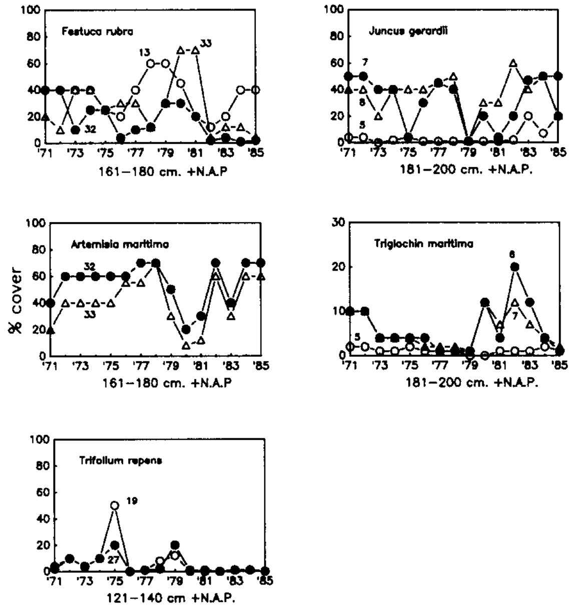

Fig. 4. Changes in degree of cover (%) of some main species in permanent plots on the salt marsh of Schiermonnikoog in the period 1971-1985. For each species the degree of cover in several plots is given, with all plots for a species situated in the same elevation class (see Table 1). The numbers correspond to the permanent plots in Table 1.

Significant correlations between the inundation frequency and the change in cover of different species were found in all elevation classes, as well as for all seasons. In order to evaluate the reaction of individual species, the significant regression coefficients were added together over all seasons for each species (Table 2). The positive and negative coefficients were added together for the first three and for the last three elevation classes (from 100–160 cm and from 161–220 cm, respectively). This resulted in overall-indices for the magnitude of the effect of inundation frequency on the cover changes of each species. Table 2 also shows whether a species has an optimal occurrence on the lower part of the salt-marsh (L), on the middle part (M) or on the dune part (D) (after Bakker & Ruyter 1981).

In the lower elevations (class 1 to 3), the change in cover of 3 out of 10 of the species present showed a positive correlation with inundation frequency, while in the upper part (elevation class 4 to 6) this was true for 6 out of 14 species (Table 2). The values of the positive indices were generally higher in the higher part of the salt marsh (Table 2). It can therefore be concluded that both the frequency and magnitude of the positive correlations were higher on the upper part of the investigated gradient. An opposite pattern was found for the negative correlations. Seven out of the 10 species occurring in the lower part showed a negative correlation with inundation frequency, whereas this was 5 out of 14 species for the upper part. The values of the negative indices were similar for both parts of the gradient.

When looking at individual species, *Festuca rubra, Triglochin maritima, Juncus maritimus* and *Juncus gerardii* showed a clear positive correlation, while *Armeria maritima, Plantago maritima, Agrostis stolonifera, Halimione portulacoides* and *Atriplex prostrata* showed a negative correlation.

Different patterns were found for the number of positive and negative correlations (summed up over the two years for each season; Fig. 5). Most positive correlations were found with the corrected inundation frequency in winter, while most negative correlations were found with the corrected inundation frequency in summer.

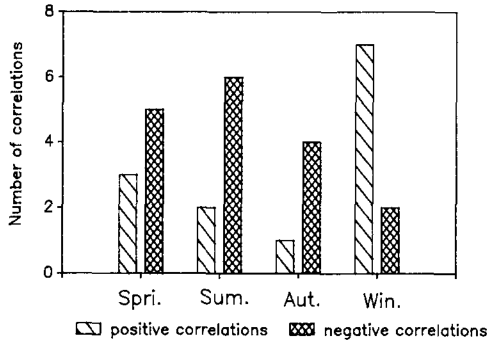

Fig. 5. The number of significant positive and negative correlations between the corrected inundation frequency and change in species cover for each season (see text).

Discussion

The pattern of correlations between the inundation frequency and change in cover of the plant species seems to be influenced by both elevation in the salt marsh and the season in which the inundations occur. Inundations had a predominantly negative effect on the cover of the different species on the lower elevations, whereas the larger positive correlations were restricted to the upper part. The mean inundation frequency decreased with the elevation on the salt marsh to about three inundations per month in the highest elevation class. Positive correlations were probably found because some species could benefit from the decline of other species. The fact that most positive correlations occurred on the higher part of the salt marsh suggests that this effect occurs mainly when the intensity of disturbance (by inundation) is relatively low.

There are several ways in which species can be positively influenced by the inundation frequency. These inundations generally reduce the cover of the vegetation by inducing anaerobiosis of the substrate, by deposition of sand and clay, or by the toxic effects of salt. Those species that frequently occur in the seed bank can have the advantage of quick re-establishment during vegetation regeneration in the gaps. This can also take place by means of vegetative reproduction of the species which are already present, e.g. by stolons or tillers. A third mechanism is a shift after inundations in the competitive relationships for light, nutrients and space, to the advantage of the more salt-tolerant species.

The results suggest that the first mechanism (re-establishment from the seed bank) partially explains the patterns of correlations that were found in this study. From the species with a large positive correlation-index (Table 2), *Festuca rubra, Juncus maritimus, Juncus gerardii* and *Artemisia maritima* occurred frequently in the seed bank on this salt marsh (Bakker 1985). From the four species with only negative correlation-indices, *Armeria maritima, Plantago maritima* and *Halimione portulacoides* were not found frequently in the seed bank (Bakker 1985).

Three other species showed positive correlations with the inundation frequency, but were not abundant in the seed bank: *Triglochin maritima, Puccinellia maritima* and *Limonium vulgare.* These species occur most frequently on the lowest part of the salt marsh (Bakker 1985), and are, therefore, expected to be more salt tolerant. A growth experiment performed by Rozema *et al.* (1985) indeed showed that these species were among the more salt tolerant ones. In a competition experiment Groenendijk *et al.* (1987) found that under saline flooding conditions *Triglochin maritima* increased its weight at the cost of *Aster tripolium* and *Puccinellia maritima.* This means that the afore-mentioned competitive replacement mechanism possibly explains the reaction of these species, but it is clear that more information is needed on the competitive relationships between salt-marsh species.

An exception to these patterns is *Atriplex prostrata,* a species which mainly occurs on the mid salt marsh in this area (Bakker 1985) in contradiction to its distribution in other coastal communities, in which it is limited to the drift line (Beeftink 1977). It showed a negative correlation but occurred frequently in the seed bank. *Atriplex prostrata* is the only annual species among those investigated, so it has to pass the seedling stage every year. This might explain its sensitivity to inundation, together with its lack of an aerenchyma system (van Diggelen 1988).

It appeared from the comparison between the seasonal effects on the correlations that most negative correlations are found with inundation frequency in summer, and most positive correlations are present with inundation frequency during the winter (Fig. 5). This means that seasonal variation in inundation frequency has to be taken into account in studies on correlations between inundation and vegetation changes (see Pehrsson 1988). A simple explanation for these seasonal differences may be that inundations during the growing season will, in general, be harmful to most species, whereas some species can take advantage of inundations in the winter through replacement mechanisms.

The statistical methods applied in this study appeared to be useful in determining the effect of fluctuations of a single environmental factor on the vegetation composition. A more complicated combination of multivariate and time-series analysis is probably needed to incorporate the effect of other factors.

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