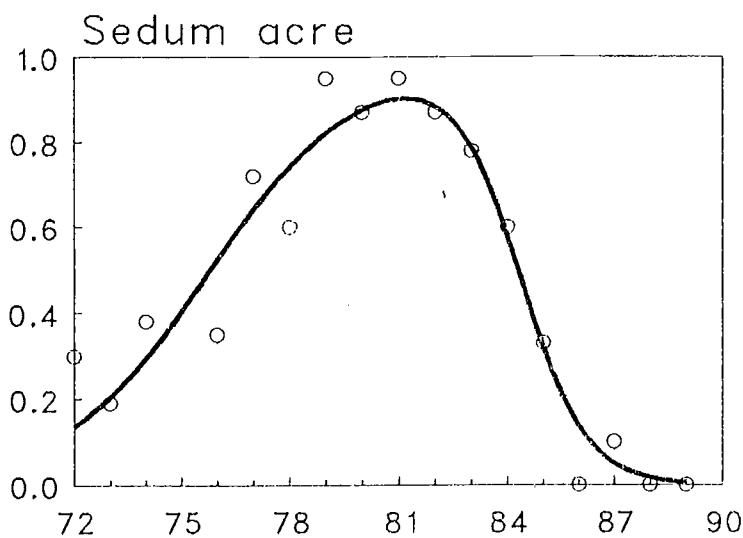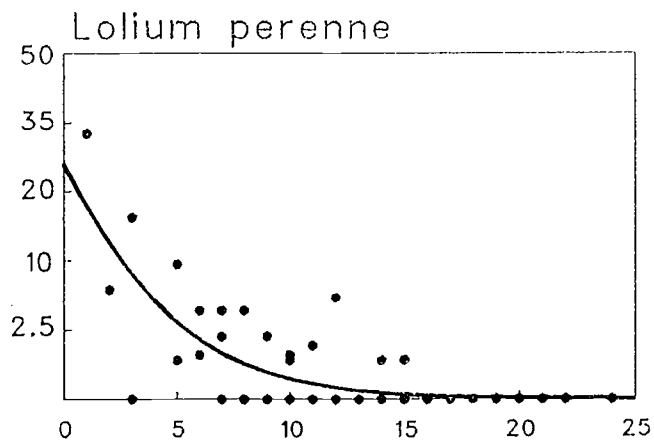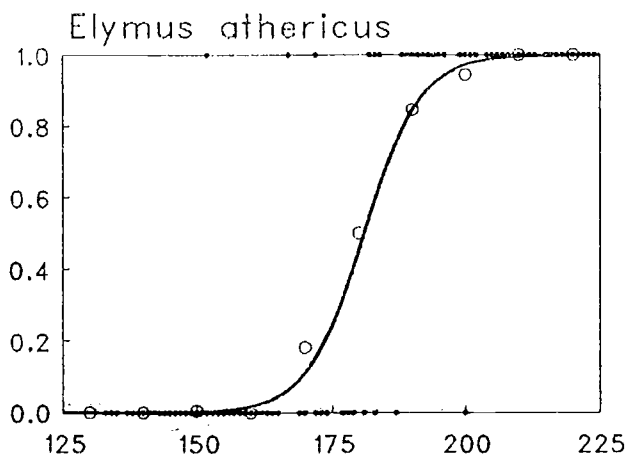# A HIERARCHICAL SET OF MODELS

# FOR

# SPECIES RESPONSE ANALYSIS

### Sedum acre

$$\frac{1}{1+e^{a+bx}} \quad \frac{1}{1+e^{c+dx}} \quad \frac{1}{1+e^{e+fx}} \quad \frac{1}{1+e^{g+hx}} \quad \frac{1}{1+e^{i+jx}}$$

### Elymus athericus

### Lolium perenne

*Jef Huisman*

# A HIERARCHICAL SET OF MODELS

## FOR

## SPECIES RESPONSE ANALYSIS

Jef Huisman

I.s.m. Han Olff & Latzi Fresco

RijksUniversiteit Groningen
Scriptie PlantenOecologie
Vakgroep Biologie van Planten
juni 1992

Abstract. Variation in the abundance of species in space and/or time can be caused by a wide range of underlying processes. Before such causes can be analyzed there is a need of simple mathematical models which can describe the observed response patterns. For this purpose a hierarchical set of models is presented. These models are applicable to positive data with an upper bound, like relative frequencies and percentages. The models are fitted to the observations by means of logistic and nonlinear regression techniques. Working with models of increasing complexity allows to choose for the simplest possible model, which sufficiently explains the observed pattern. The models are particularly suited for description of responses in time or over major environmental gradients. Deviations from these temporal or spatial trends may be statistically ascribed to, for example, climatic fluctuations or small-scale spatial heterogeneity. The applicability of this approach is illustrated by examples from recent research. A combination of simple, descriptive models like those presented in this paper and causal models as developed by several others, is advocated as a powerful tool towards a fuller understanding of the dynamics and patterns of vegetational change.

## Introduction

Responses of organisms in space and/or time may be the consequence of physiological limitations, of interactions with other organisms, of human interference and so on. But, whatever the causes of a response, there will be a need of simple mathematical models which can describe the observed relationships. One of the classical and frequently used models is the bell-shaped Gaussian response curve (Gauch & Whittaker 1972; ter Braak & Looman 1986). However, usually there are no a priori reasons to assume that organisms should respond in the form of such symmetrical curves (e.g., Austin 1976). Austin (1990) discusses several examples of skewed curves in relation to factors like temperature, soil organic matter and total soil nitrogen. Succession series will often yield asymmetric curves of species abundance versus time. In particular, successions may proceed to a steady state of species abundances. It can be concluded that response types will differ among organisms and factors studied. Therefore, descriptions of the observed relationships should incorporate the possibility to distinguish between different response types.

Furthermore, many species will exhibit considerable variation around the observed response. Relationships between fluctuations in the major species composition of plant communities and fluctuating abiotic conditions have been frequently observed (e.g., Talbot, Biswell & Hormay 1939; Watt 1960; van der Maarel 1981; Cramer & Hytteborn 1987). Only a few studies, however, have examined and quantified these relationships through statistical analyses (e.g., Pitt & Heady 1978; van Tooren, Schat & ter Borg 1983; Collins, Bradford & Sims 1987; de Leeuw, Olff & Bakker 1990). Still fewer studies distinguished between long-term trends and short-term fluctuations. If fluctuations in the species composition are superimposed on major successional trends, statistical detrending will often be required before fluctuating species abundances can be related with, for example, fluctuating weather factors (e.g., Cashen 1947; Hunt, Hope-Simpson & Snape 1985).

Species response curves may help both the examination and quantification of suggested relationships. For this purpose, a hierarchical set of descriptive models is presented. Examples illustrate how these models may be used for the exploration of spatial and temporal variation in species composition.

# The models

## *Qualitative presentation of the models*

Percentages and frequencies, the data types often used in vegetation science, impose a certain structure on the response models to be used. For example, a linear relationship between percentage cover of a certain species and an environmental variable cannot hold ad infinitum, because the cover cannot exceed 100%. The models presented here are particularly suited for such positive data types with an upper bound, like frequencies, percentages and other positive data on which a maximum M can be imposed. The models are ranked according to the increasing complexity of biological information contained (Fig. 1):
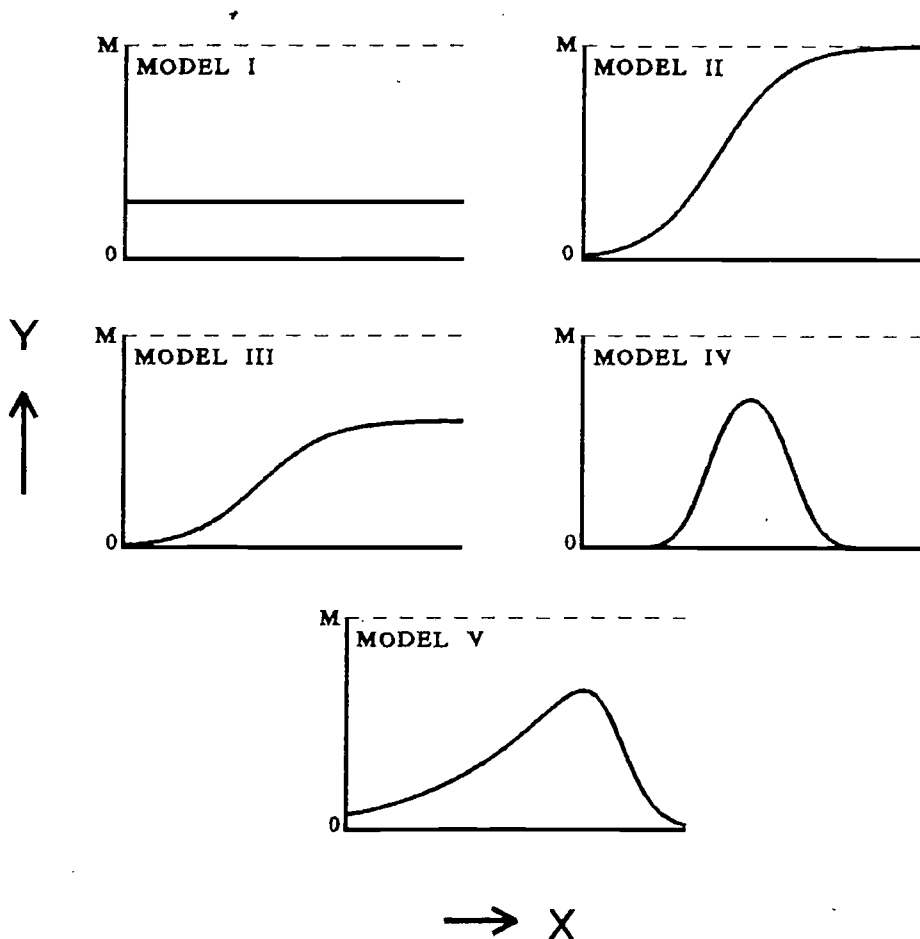


Fig.1: A set of five simple response models, ranked by their increasing complexity. Model I: no trend. Model II: increasing or decreasing trend. Model III: increasing or decreasing trend bounded below the maximum attainable response M. Model IV: symmetrical response curve. Model V: skewed response curve.

model I:      no significant trend in space or time.

model II:     an increasing or decreasing trend where the maximum is
              equal to the upper bound M.

model III:    an increasing or decreasing trend where the maximum is
              below the upper bound M.

model IV:     increase and decrease by the same rate
              (symmetrical response curve).

model V:      increase and decrease by different rates
              (skewed response curve).

More complex models, like bimodal curves, will not be discussed here.
Data types with an upper and lower bound are inherently nonlinear.
Because this structure is a priori included in the presented models,
the models will certainly not be suited for all data. Plant biomass,
for example, may be limited by abiotic and biotic constraints, but
the data type itself, mass, is not limited by any maximum. For such
data, model II may be better represented by an increasing or decreasing
trend without any maximum than by our representation. Thus for data
types without a logical upper bound, it is advisable to develop another,
but analogous, hierarchical set of models.

Working with models of increasing complexity allows to choose for
the simplest possible model, which sufficiently explains the observed
pattern. In fact this is just the normal approach in multiple regression:
an additional parameter is only incorporated if it can explain a
significant part of the remaining variation.


*Specification of the models*

The models of Figure 1 may be described by several different equations.
The skewed curve of model V, for example, may be fitted to high-order
polynomial functions, a power Gaussian equation (Olff & Bakker 1991),
a beta-function (Austin 1976) or the product of two logistic functions.
When descriptive models are considered, there are no a priori reasons
to assume that one equation should be better than the other. The validity
of descriptive models should be obtained from their applicability in
many situations. However, the possibility to attain values which are
unrealistic is an important objection against certain equations. A
curve describing changes in, for example, probability of occurrence

should not be able to yield negative values or exceed one. Furthermore, third- or higher order polynomials may yield biologically unrealistic curves no longer restricted to the relationships of Figure 1.

The following consistent set of logistic equations can be used for positive data with an upper bound M:

model I: $\qquad y = M \dfrac{1}{1 + e^{a}}$ $\qquad\qquad\qquad\qquad$ (1)

model II: $\qquad y = M \dfrac{1}{1 + e^{a+bx}}$ $\qquad\qquad\qquad$ (2)

model III: $\qquad y = M \dfrac{1}{1 + e^{a+bx}} \dfrac{1}{1 + e^{c}}$ $\qquad\qquad$ (3)

model IV: $\qquad y = M \dfrac{1}{1 + e^{a+bx}} \dfrac{1}{1 + e^{c-bx}}$ $\qquad\qquad$ (4)

model V: $\qquad y = M \dfrac{1}{1 + e^{a+bx}} \dfrac{1}{1 + e^{c+dx}} \; ,$ $\qquad$ (5)

where b and d have opposite signs.

Y and x are the response and the explanatory variable respectively; a, b, c and d the parameters to be estimated, and M a constant which equals the maximal value which can be attained (e.g., for relative frequencies M = 1, for percentages M = 100). Note that model IV and V are represented by an interaction of two logistic terms, where one term describes the increasing part of the curve and the other term describes the decreasing part.

Qualitatively, model IV may also be represented by a Gaussian logit curve (sensu ter Braak & Looman 1986):

$$y = M \dfrac{1}{1 + e^{a+bx+cx^2}} \; ,$$ $\qquad$ (6)

where c > 0.

For reasons of consistency with respect to the other models, we prefer (4) to (6).

*Fitting the models*

   In this section, we discuss the regression techniques on which the
parameter estimates and appropriate choice of the models should be
based. A major distinction is made between the analysis of continuous,
quantitative data (least-squares regression) and binary, 'presence/
absence' data (logistic regression).

   Since the presented models differ in the number of parameters to
be estimated, it can be tested whether an increase in the number of
parameters yields a significantly better fit. Model III and model IV,
however, contain the same number of parameters. Thus a choice between
these two models cannot be based on any significant improvement of
the fit. Whenever this choice is necessary, the model with the best
fit should be selected. All models should be calculated, since it might
happen that model V yields a significantly better fit than model I,
whereas model II, III and IV do not.


1. Continuous data:

   For continuous, quantitave data types like percentage cover, the
parameters of the presented models can be estimated by nonlinear
regression. In nonlinear regression, just as in linear regression,
the residual sum of squares of observed response versus predicted
response is minimized. However, in contrast with linear regression,
there is no analytical solution for the minimum of the residual sum
of squares. Instead, the residual sum of squares is minimized by
iteration. A commonly used method (e.g., SAS 1988; SPSS 1990) is
Marquardt's (1963) algorithm, described in detail by Conway, Glass
& Wilcox (1970). Numerical procedures for the estimation of parameters
by nonlinear regression might sometimes encounter local optima. If
the estimation of parameters is distrusted, the use of different starting
conditions in the iteration can be recommended.

   The proportion of variance 'explained' by the model is given by

$$R^2 = 1 - \frac{residual\ sum\ of\ squares}{total\ sum\ of\ squares} , \tag{7}$$

where $R^2$ is the coefficient of (multiple) determination. For nonlinear
models the usual tests for linear models are not exact, even under
the assumption of independent, homoscedastic normal errors. But in
large samples they are still fairly robust against nonnormality (Miller
1986). Moreover, for percentages an $\arcsin(\sqrt{y}/100)$ transformation might
improve the homoscedasticity of the data (Sokal & Rohlf 1981; Miller
1986). (In that case, $M = \arcsin(\sqrt{1}) = 90$ ). Hence, since there is no
workable, reasonable alternative, we propose to use the F statistic

with the usual tabulated critical values to test whether an increasing
number of parameters yields a 'significant' increase of $R^2$:

$$F_{K,N-J-K} = \frac{(R^2_{new} - R^2_{old})}{(1 - R^2_{new})} \frac{(N - J - K)}{K} \quad , \tag{8}$$

where N is the total number of observations, $R^2_{old}$ represents $R^2$ of a
model with J estimated parameters and $R^2_{new}$ represents $R^2$ of a model with
J+K estimated parameters (e.g., Sokal & Rohlf 1981; Jongman, ter Braak
& van Tongeren 1987). If this $F_{K,N-J-K}$ is significant, the new model with
J+K parameters is chosen.


2. Binary data:

   In many ecological studies only presence/absence or other binary
('yes/no') data are obtained. The observation is either 'present' (y=1)
or 'absent' (y=0), thus the error structure is specified by the Binomial
distribution. The probability p that the object is present can be
estimated. A trend represents a change of p with a change of an
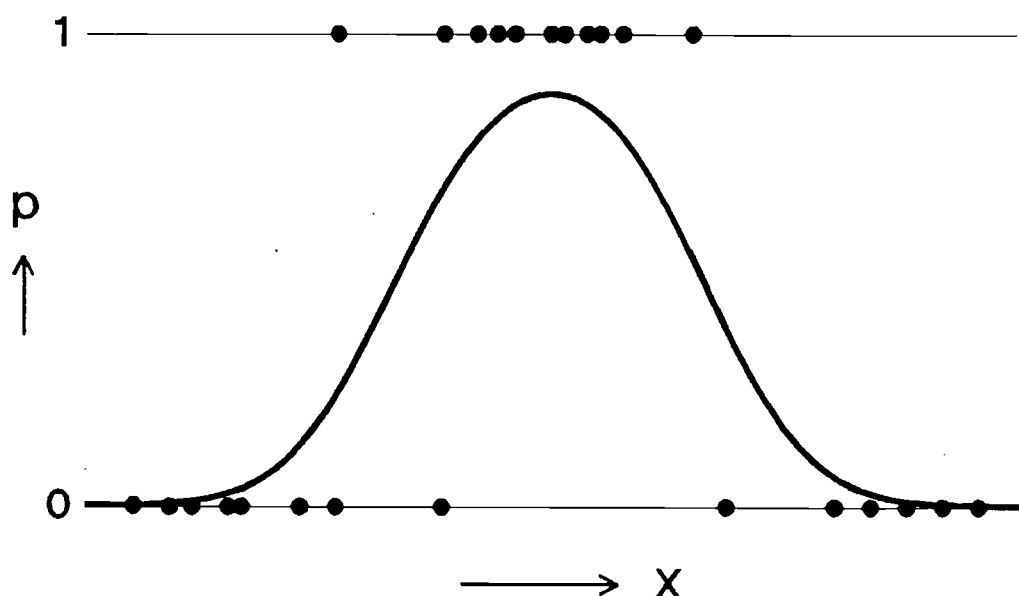explanatory variable (Fig. 2).



Fig.2: Fitting presence/absence data by logistic regression. The
probability of occurrence (p) is related to a certain variable x.

In case of binary data, the parameters of a model are estimated by logistic regression (e.g., ter Braak & Looman 1986; Jongman, ter Braak & van Tongeren 1987; McCullagh & Nelder 1989). Logistic regression minimizes the statistic -2LL (where LL stands for "Log-Likelihood"), also known as the deviance, by iteration. This statistic is given by

$$-2LL = -2\sum_{i=1}^{N} \ln(L_i) \ , \qquad (9)$$

where N is the total number of observations, and $L_i$ is the predicted probability of observation i. Suppose, for example, that the probability to find a certain species is predicted to be 0.8, then, when this species is found $L_i = 0.8$, but when it is not found $L_i = 0.2$.

The use of -2LL itself for assessing the adequacy of the model is usually not valid. But it can be tested whether addition of K extra parameters yields a significant reduction of -2LL, because the reduction of -2LL is asymptotically distributed as a $\chi^2_K$ distribution:

$$\chi^2_K = (-2LL_{old}) - (-2LL_{new}) \ , \qquad (10)$$

where $-2LL_{old}$ represents -2LL of a model with J estimated parameters and $-2LL_{new}$ represents -2LL of a model with J+K estimated parameters. If this $\chi^2_K$ is significant, the new model with J+K parameters is chosen. It should be stressed that this approach is an approximation, it is only valid if N is large (McCullagh & Nelder 1989).

Unfortunately, up to now statistical software packages like BMDP (Dixon 1985), SAS (1988) and SPSS (1990) only allow to estimate parameters of equations (1), (2) and (6) by logistic regression. As an alternative, the parameters of (3), (4) and (5) may be estimated by nonlinear regression. But this is not an optimal solution, since the residual sum of squares is minimized instead of -2LL. For binary data, the CURVE module of VEGROW (Fresco 1991) minimizes -2LL of all models by iteration. A commercial version of VEGROW is available upon request from the last author.

For continuous data the proportion of variance 'explained' by the model is given by $R^2$. For binary data -2LL is used to discriminate between the models. Unfortunately, however, -2LL does not give much insight in the explained variation. A large value of -2LL cannot be considered evidence of a poor fit (McCullagh & Nelder 1989). Calculation of the relative reduction of -2LL, analogous to (7), is not very informative; its value will usually be low because the observations ("0" and "1") necessarily deviate from the values of p (0<p<1). As an alternative, we propose to use $R^2$ after the data have been subdivided over several intervals (see examples). Then $R^2$ can be calculated following (7), where the observed response is represented by the relative frequency in each

interval. Since the value of $R^2$ will depend on the interval division, this is a rather subjective method. But calculation of $R^2$ for binary data may be useful when the model fits of different species responses along the same gradient are compared. Annual plant species, for example, will often exhibit more fluctuations around a major successional trend, i.e. have a lower $R^2$, than perennials.

## Residuals

Many species will exhibit considerable variation around the observed response. This may be due to sampling errors or to some stochasticity in the studied phenomena, but also to variation of variables not included in the model. Deviations from successional trends may be the consequence of, for example, climatic fluctuations. Deviations from spatial trends might indicate small scale heterogeneity superimposed on major environmental gradients. In order to investigate the possible causes of such deviations, the influence of the trend must first be eliminated. This can be performed by different methods (McCullagh & Nelder 1989; SPSS 1990). For linear models the residuals (the difference between observed response and predicted response) are often used. If, for continuous data, a data transformation has improved the homogeneity of the error variance, then the residuals should be derived from the transformed data.

For binary data, where the variance changes with the probability of occurrence p, standardized residuals (SR) might be more appropriate:

$$SR = \frac{residual}{\sqrt{p(1-p)}} ,$$

(11)

where p represents the probability of occurrence predicted by the calculated trend. Note that $\sqrt{p(1-p)}$ is the standard deviation of a binomial distribution with N=1.

These residuals may be correlated with the variables considered responsible for the deviations from major trends.

## Examples

In this section we will shortly discuss several examples from recent research. All calculations were done using the CURVE module of VEGROW (Fresco 1991), a program package developed for the analysis of vegetation data, which follows the procedures described above.

In the Drentse Aa study area (The Netherlands, 53°NL, 6°40' EL) a hay field succession was studied, which started after cessation of fertilizer application. Fertilizer application was stopped in order to restore former species-rich hay field communities, which were found before agricultural practices were intensified (Bakker 1989). Three different fields are used in this example, in which permanent plots of 2x2 m. have been recorded from 1972 onwards. Two fields had four plots, while one field had two plots. Fertilizer application was stopped in 1966 (one field) and in 1972 (two fields), respectively. To account for the different numbers of plots per field and to exclude pseudoreplication (Hurlbert 1984), the mean percentage cover per field was used as the dependent variable, and age (years without fertilizer application) was used as the independent variable. Percentage cover was arcsin($\sqrt{y}/100$) transformed prior to the analysis, which improved the homogeneity of the error variance considerably.

Table 1: The presented logistic models fitted on continuous data of *Ranunculus repens* from the hay field succession of the Drentse Aa (N=47). Model IV fitted significantly better than model I and model II, model IV had a higher $R^2$ than model III, and model V did not fit significantly better than model IV.

| Model | $R^2$ | d.f. |
|-------|-------|------|
| I | 0 | 46 |
| II | 0.002 | 45 |
| III | 0.075 | 44 |
| IV | 0.202 | 44 |
| V | 0.203 | 43 |

| Model | Model tested against | $F_{K,N-J-K}$ | Test d.f. K | N-J-K | p |
|-------|------|------|------|------|------|
| IV | I | 5.58 | 2 | 44 | <.01 |
| IV | II | 11.07 | 1 | 44 | <.01 |
| IV | III | – | – | – | – |
| V | IV | 0.05 | 1 | 43 | >.1 |

In Table 1 *Ranunculus repens* is given as an example. Model IV fits significantly better than model I and model II. As discussed above, a choice between model III and model IV cannot be based on any statistical significance, since they do not differ in the number of parameters. But model IV has a much higher $R^2$ than model III. Model V does not fit significantly better than model IV. Therefore, model IV is chosen. The calculated trends of *Ranunculus repens* and three other species are given in Figure 3. From Figure 3a it is clear that description of the decreasing abundance of *Lolium perenne* by model III, IV or V will not increase our information. Model II is the simplest model, which still sufficiently describes the observed successional pattern of *Lolium perenne*. *Ranunculus repens* increased towards mid-succession and then decreased at the same rate (model IV). *Agrostis capillaris* and *Carex nigra* started to increase later and did not show any consistent change during the latest years of this succession series (model III). This succession has been studied in further detail on the physiological (Olff 1992) and ecosystem level (Olff & Bakker 1991).
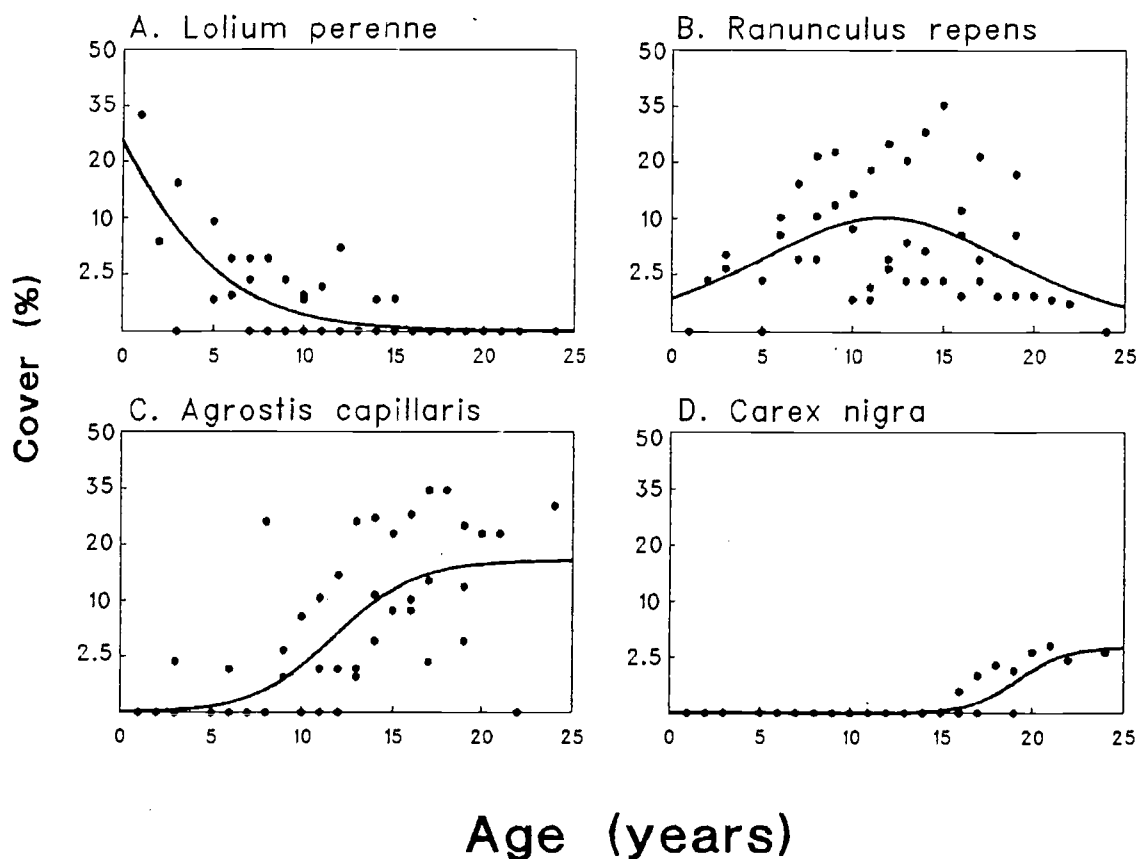


## Age (years)

Fig.3: Percentage cover during the hay field succession at the Drentse Aa (plotted on an arcsin($\sqrt{y}$) scale). The calculated trends are based on 47 observations (closed dots) from three hay fields. (A) *Lolium perenne* (model II; $R^2=0.59$), (B) *Ranunculus repens* (model IV; $R^2=0.20$), (C) *Agrostis capillaris* (model III; $R^2=0.46$), (D) *Carex nigra* (model III; $R^2=0.73$).

*Spatial trends from binary data: a salt marsh gradient*

On the Dutch island of Schiermonnikoog (53°29' NL, 6°12'EL) the vegetation along an elevational gradient on the salt marsh was studied. Lower parts of the salt marsh are more frequently inundated by tidal waters. A 11 x 51 meter grid was laid out, which was subdivided in 561 plots of 1 m². In each plot, the three most abundant plant species were recorded, which were referred to as the dominants of the vegetation. Furthermore, the elevation of the centre of each quadrat with respect to standard sea level (NAP, Dutch ordnance level) was determined. The species data were interpreted as binary data (dominant or not) and related to elevation. An example is given for the perennial grass species *Festuca rubra* (Table 2, Fig. 4c). As discussed above, for binary data it is not valid to asses the adequacy of each model from -2LL itself (i.e. the upper part of Table 2). But reduction of -2LL provides a method for testing the significance of additional parameters (i.e. the lower part of Table 2). Model V fits significantly better than the simpler models.

Table 2: The presented logistic models fitted on binary data of *Festuca rubra* along a salt marsh gradient on Schiermonnikoog. Based on 561 plots of 1 m². Model V had the best fit of all models tested and all terms in this model significantly reduced -2LL.

| Model | -2LL | d.f. |
|-------|------|------|
| I | 767.1 | 560 |
| II | 766.4 | 559 |
| III | 766.3 | 558 |
| IV | 572.1 | 558 |
| V | 406.0 | 557 |

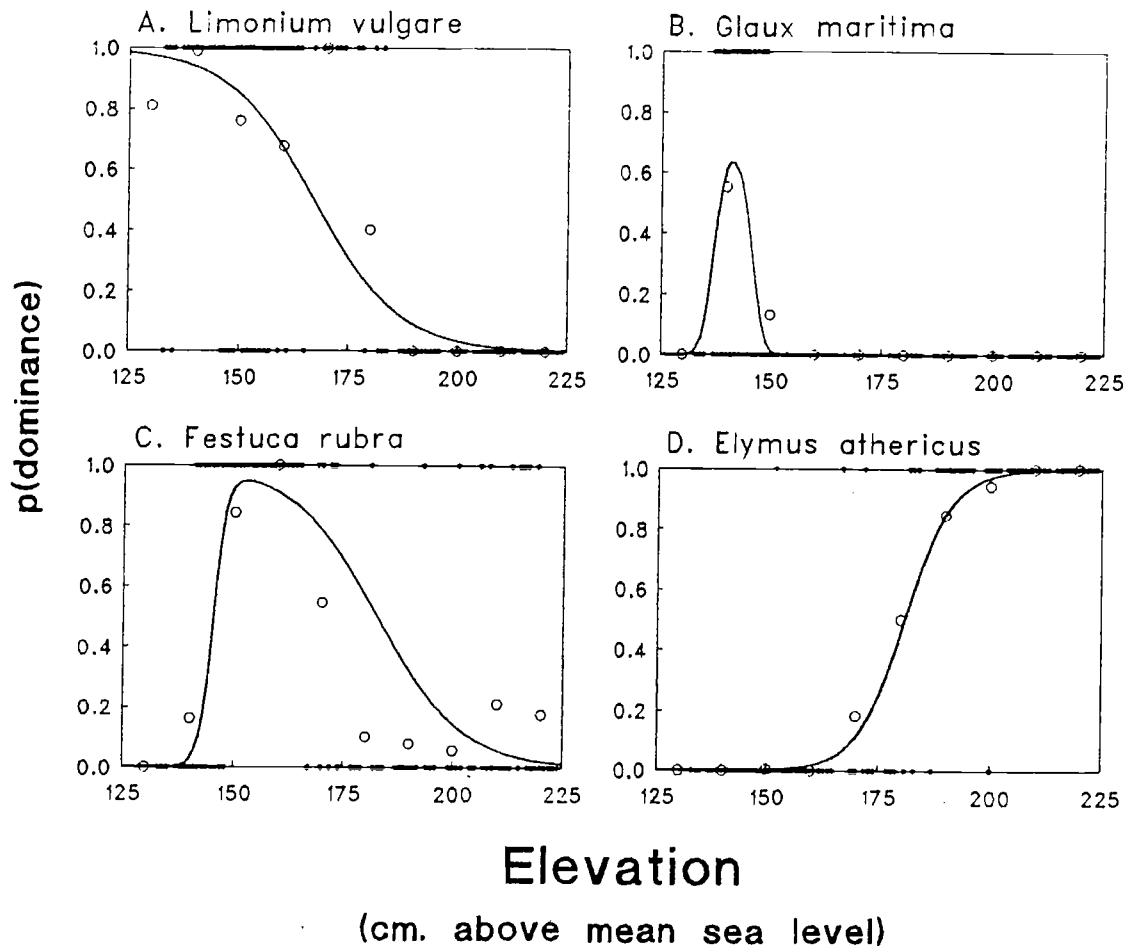| Model | Model tested against | -2LL reduction $(\chi^2_K)$ | Test d.f. K | p |
|-------|------|------|------|------|
| V | I | 361.1 | 3 | <.001 |
| V | II | 360.4 | 2 | <.001 |
| V | III | 360.3 | 1 | <.001 |
| V | | | | |

## Elevation
### (cm. above mean sea level)

Fig.4: Probability of dominance along a gradient from the low salt marsh to the high salt marsh of Schiermonnikoog. Based on 561 plots of 1 $m^2$ (small closed dots). The open dots indicate the fraction of plots in which the species dominated, for each 10 cm. interval. (A) *Limonium vulgare* (model II; $R^2=0.76$), (B) *Glaux maritima* (model IV; $R^2=0.94$), (C) *Festuca rubra* (model V; $R^2=0.62$), and (D) *Elymus athericus* (model II; $R^2=0.99$).

The calculated response curves of *Festuca rubra* and three other species are depicted in Figure 4. The curves were computed using the binary data (small closed dots). However, these binary data yield little information on the fit of the curves. Therefore, the factor elevation was subdivided in 10 intervals of 10 cm each. For each interval the fraction of plots in which the species was dominant was computed (open symbols in Fig. 4). This shows that there is good agreement between the observed dominance fractions and the calculated trends. *Limonium vulgare* dominated the lowest plots, and gradually decreased toward the higher elevations (model II). *Glaux maritima* showed an optimum, relatively low on the gradient (model IV). Somewhat higher, *Festuca rubra* showed an optimum, which was clearly skewed (model V). For this species, we can hypothesize that its dominance along the gradient is determined by different processes, resulting in such a skewed

distribution. For salt marsh gradients in general it is thought that the lower limits of species distributions are determined by the physiological tolerances of species to extreme values of physical factors (salinity, anaeroby), while competitive interactions are considered more important in determining the upper limits (Snow & Vince 1984). *Elymus athericus* dominated the highest plots on the gradient (model II) and, in view of its plant height and clonal growth, could be one of the species which has a competitive superiority over *Festuca rubra* in this situation (Bakker 1989).

*Trends and fluctuations during a primary succession*

On the same island, Schiermonnikoog, a primary succession has been studied (van Tooren, Schat & ter Borg 1983; Olff, Huisman & van Tooren subm.). In 1959 this succession was initiated with the building of a sand dike, which sheltered a bare 'beach plain' with scattered young dunes from frequent flooding by the North Sea. From 1972 onwards the presence of all plant species was recorded yearly in 240 plots of 0.4 $m^2$. Thus the data set consists of binary data. The plots were subdivided over different elevation classes ('Plains', 'Slopes' and 'Dunes'), to account for the spatial variation. For each elevation class the species responses in time were fitted to the presented models. Furthermore, for each elevation class the yearly observed probability of occurrence of each species was calculated, which represents the fraction of the 0.4 $m^2$ plots in which the species was actually observed. Consider *Sedum acre*, a small perennial on the Dunes. Model V fitted significantly better than the simpler models. As can be seen in Figure 5a, there is a close agreement between the yearly observed probability of occurrence and the trend 'predicted' by model V. It is concluded that *Sedum acre* first increased and then decreased, where the rate of increase differed from the rate of decrease. In fact, the underlying processes were different. First sandblowing may have prevented *Sedum acre* from establishing. Later onwards small species such as *Sedum acre* and *Cerastium semidecandrum* were outshaded by taller species, particularly by the shrub *Hippophae rhamnoides* (Olff, Huisman & van Tooren subm.; Fig. 5b).
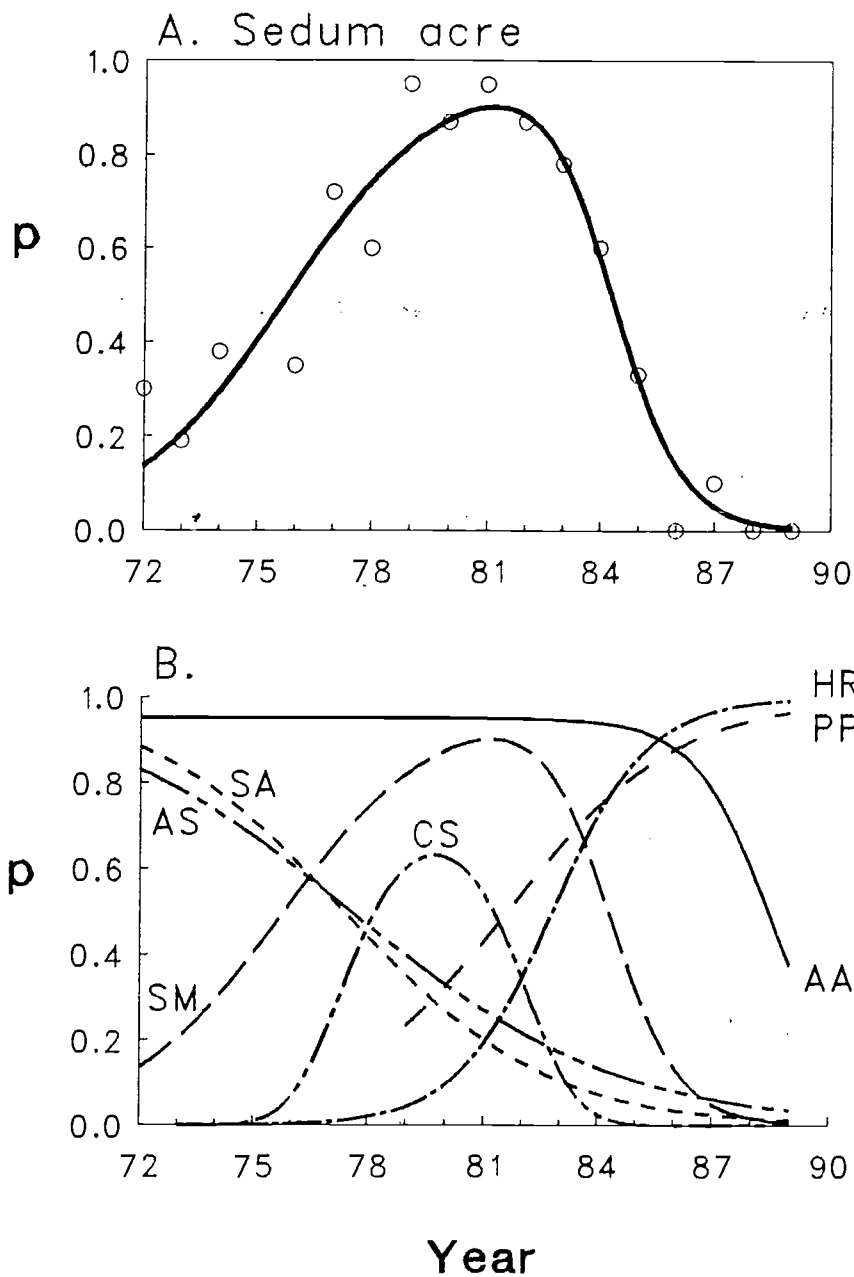
**A. Sedum acre**



**B.**

**Year**

Fig.5: Probability of occurrence (p) on the Dunes of Schiermonnikoog during primary succession. Based on 32 permanent plots of 0.4 $m^2$.

(A) *Sedum acre* (model V; $R^2=0.95$). Open dots indicate the yearly observed probability of occurrence.

(B) Model II: AS = *Agrostis stolonifera* ($R^2=0.74$), HR = *Hippophae rhamnoides* ($R^2=0.98$), PP = *Poa pratensis* ($R^2=0.90$), and SA = *Sonchus arvensis* ($R^2=0.88$), model III: AA = *Ammophila arenaria* ($R^2=0.73$), model IV: CS = *Cerastium semidecandrum* ($R^2=0.80$), model V: SM = *Sedum acre* ($R^2=0.95$).

16

The analysis of deviations from major trends is illustrated by the same primary dune succession. During heavy storms in winter the Plains can still be flooded by seawater, both from the north via openings in the sand dike and from the south via the saltmarshes (the area may be compared with a bath-tub). Extremely high tides (see Fig. 6a) result in the formation of many large gaps in the perennial vegetation of the Plains. Several annual species, mainly halophyts, can establish in these gaps. Thus superimposed on the successional trends, large year-to-year fluctuations of these annual species were observed, which was illustrated by their low $R^2$ (see Fig. 6b for an example). The standardized residuals from the trends of many annual halophytes could indeed be correlated with the maximal heights of the sea level (Table 3; Fig. 6c). Furthermore, fluctuations of short-lived glycophytes were negatively correlated with rainfall deficit in spring (Table 3), where the rainfall deficit is calculated as precipitation minus evaporation according to Penman (1948). In this study area, a high rainfall deficit causes a low soil moisture content and an increased salinity (van Tooren, Schat & ter Borg 1983). Both low soil-moisture content and high salinity have negative effects on the germination and establishment of most of these short-lived glycophytes (Schat 1982).

Table 3: Partial regression coefficients of the standardized residuals of the calculated trends against annual maximal height of the sea level (F), and rainfall deficit in spring (R). Examples from 8 species are given. Based on 18 years recording of a primary succession in a coastal dune area. - = no trend calculated, because species occurred in less than 4 years, n.s. = $p > .05$, * = $p < .05$, ** = $p < .01$

| | PLAINS | | DUNES | |
|---|---|---|---|---|
| | F | R | F | R |
| Halophytes | | | | |
| *Salicornia spec.* | 0.61** | n.s. | – | – |
| *Spergularia spec.* | 0.68** | n.s. | – | – |
| *Suaeda maritima* | 0.63* | n.s. | – | – |
| *Atriplex prostrata* | 0.54* | n.s. | – | – |
| Glycophytes | | | | |
| *Centaurium pulchellum* | n.s. | -0.57* | – | – |
| *Centaurium littorale* | n.s. | -0.63* | n.s. | n.s. |
| *Odontites verna* | n.s. | n.s. | n.s. | -0.60* |
| *Arenaria serpyllifolia* | – | – | n.s. | -0.77** |

17

A. Max. sea level
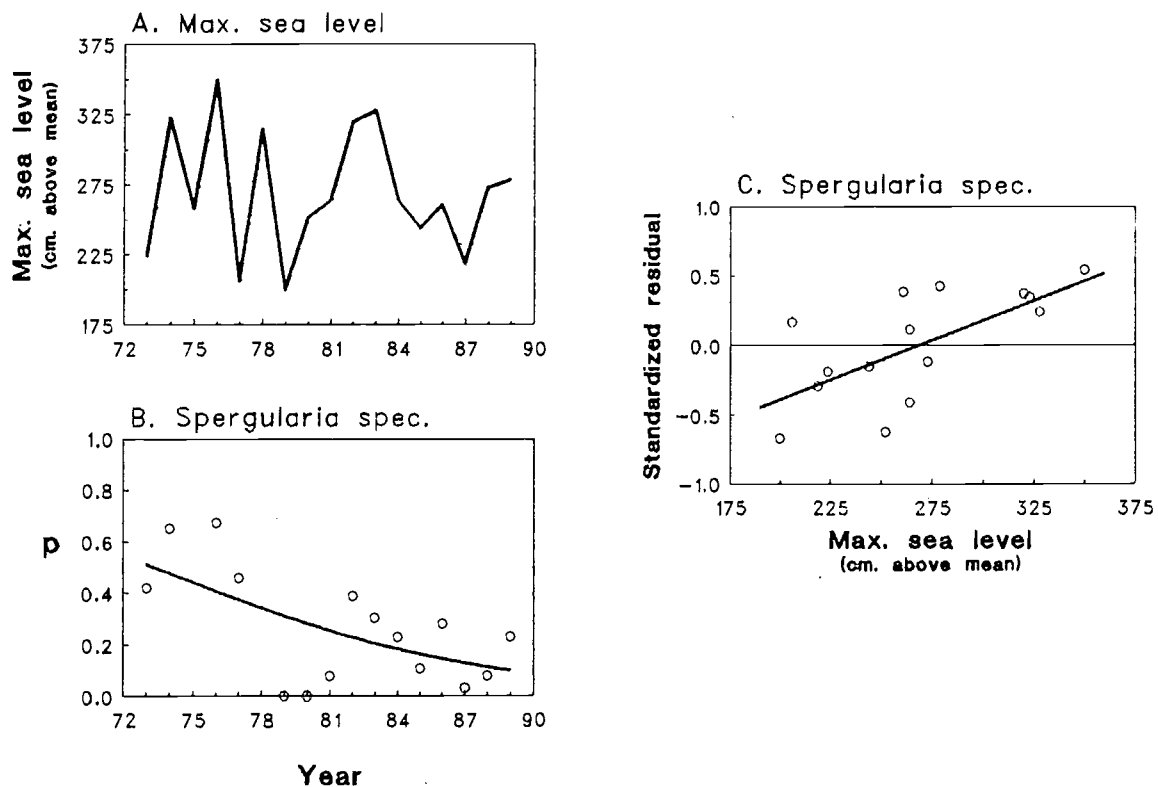
B. Spergularia spec.

C. Spergularia spec.

Year

Fig.6: (A) 'Annual' maximal height of the sea level. All 'annual' highest floodings occurred in the autumn and winter preceding the growing season; years indicate these growing seasons.

(B) Probability of occurrence (p) of *Spergularia spec.* on the Plains of Schiermonnikoog during primary succession (model II; $R^2=0.40$). Based on 132 permanent plots of 0.4 $m^2$. Open dots indicate the yearly observed probability of occurrence.

(C) Correlation between standardized residuals of the calculated trend of *Spergularia spec.* on the Plains (Fig. 5A) and annual maximal height of the sea level ($R^2=0.46$; N=15; p<.01).

18

Discussion

The calculated trends can provide much information. The type of response, the maximal species response, the species optimum (i.e. the value of the explanatory variable at which the species response is maximal) and the skewness of the response can all be derived in a standardized way. Often one is also interested in the response breadth of a species (sometimes also referred to as "tolerance" or "ecological amplitude"). It is obvious that model I, II and III can only indicate the minimal response breadth. The symmetric Gaussian response curve, model IV, provides an elegant measure of the response breadth analogous to the standard deviation of a normal distribution (ter Braak & Looman 1986). If, however, responses are skewed, as in model V, the choice of an appropriate measure of the response breadth becomes rather arbitrary in the sense that different measures may yield quite different results. One might define response breadth as the interval length of the explanatory variable along which the response remains above a certain threshold value. This threshold value may be absolute (e.g., coverage > 5%) or may be related to the maximal response attained by a species (e.g., coverage > 5% of maximal coverage attained). Measures analogous to Simpson's equitability index and Shannon's diversity index, derived from information theory, have also been used (Levins 1968; Bazzaz 1987). We prefer to use the threshold measures in view of their clearcut, direct interpretation in terms of the explanatory variable.

The same set of equations was applied to three completely different examples. In contrast, causal models usually require different equations for different types of explanatory variables. But there is no objection against application of the same set of equations to different environmental gradients as long as the models are only used for description.

The models were related to only one variable. This variable could explain (in a statistical sense) most variation in the observed response, and other variables were only introduced to account for deviations from the trend. Description of the response by only one variable can be useful even if the response might be determined by many underlying processes, as for the successional response of *Sedum acre* or for the spatial distributions of species along a salt marsh gradient. But the models may also be extended to two or three different variables (see Austin, Cunningham & Fleming 1984; Jongman, ter Braak & van Tongeren 1987). This will be particularly useful if it may be assumed that only a few variables are responsible for most of the observed variation. Van Dam et al. (1986), for example, used a multiplicative model analogous to model V, where one term described the effect of habitat destruction

19

and the other term the effect of air pollution. In our example of the primary succession, a multiple regression could have been performed with both time $(x_1)$ and elevation $(x_2)$ as the explanatory variables, e.g.,

$$y = M \frac{1}{1 + e^{a+bx_1}} \frac{1}{1 + e^{c+dx_1}} \frac{1}{1 + e^{e+fx_2}} \frac{1}{1 + e^{g+hx_2}} . \qquad (12)$$

Unfortunately, skewed relationships with respect to only two variables are already hard to analyze statistically, because of the great number of parameters to be estimated. For this reason the permanent plots of the primary succession example were subdivided over different elevation classes, which reduced the regression problem to only one variable, time. If one is interested in the explicit inclusion of many variables, ordination techniques like canonical correspondence analysis will be more appropriate (Jongman, ter Braak & van Tongeren 1987). But a priori inclusion of many variables is no guarantee for a better understanding of the actual response. Most ordination techniques use very simple response models, such as the weighted average or the symmetrical Gaussian response curve (model IV). It should therefore be realized what is more relevant in a particular situation: the broad relationship with many factors, or a detailed description with respect to one or only a few variables (see also ter Braak & Prentice 1988).

Usually it is not known a priori whether the observed response will indeed be a member of the five presented models. Bimodal curves, for example, were not included. The qualitative shape of the response can be examined by a simple plot of the observations, but also by the so-called Generalized Additive Models (GAMs) recently illustrated by Yee & Mitchell (1991). GAMs are nonparametric models, based on smoothers, which can suggest a particular shape of the response model. It can be tested whether the unspecified smooth functions of a GAM can be replaced by one of the parametric models presented in this paper. If these parametric models are 'statistically allowable' then for reasons of parsimony they are to be preferred (Yee & Mitchell 1991).

Curve fitting, for example by minimizing the residual sum of squares, is an often used technique for the analysis of time series (Chatfield 1989). However, the F and $\chi^2$ test, used to discriminate between the five different models, assume independent error terms (e.g., Miller 1986). Thus, for succession series, the choice of the most appropriate model may be hampered by the biological and statistical dependence of an observation in a given year on observations of the same object in the previous years (temporal autocorrelation). But this is not a general objection against the use of regression techniques for the analysis of succession series. Not seldom serial dependence of the

residuals may be assumed negligible, see for example *Sedum acre* (fig.5A).
Autocorrelation may also be reduced by combining data from different
fields with different ages, as in the hayfield example. Furthermore,
several statistical techniques have been developed to cope with
autocorrelation. Time-dependent patterns can be modeled by spectral
analysis (also known as Fourier analysis) or Box-Jenkins time series
analysis (Box & Jenkins 1976) if these patterns are parts of repeatable
'cyclic' events. Spectral analysis, for example, may be a valuable
tool for the detection of deviations from the normal tidal cycle. These
deviations may have profound influences on species composition and
can be correlated with fluctuations in species abundance analogous
to the methods described in the 'Residuals' section (Olff, Bakker &
Fresco 1988). But spectral analysis and Box-Jenkins methods are primarily
used to detect and describe cyclic phenomena, while they are less
suitable for describing long-term trends superimposed on the cycli.
Often, however, species abundances along temporal or spatial gradients
will not show repeatable, cyclic patterns, but a 'simple' unimodal
response. Another approach might be to use tests for dependent data.
These tests are often modifications of the usual tests for independent
data, corrected for the error dependence (e.g., Miller 1986; El-Shaarawi
& Damsleth 1988; Clifford, Richardson & Hémon 1989). Valid tests can
also be constructed by special schemes for permutation of residuals
that do not modify the autocorrelation structure (Besag & Clifford
1989; ter Braak 1992).

The proposed approach offers the possibility to separate long-term
trends and short-term fluctuations. During the primary succession of
Schiermonnikoog, for example, the accumulation of nitrogen is considered
to be an important determinant of the successional dynamics, favouring
taller species in later, nitrogen-richer stages (Olff, Huisman & van
Tooren subm.). But salinity, moisture content and flooding are considered
to be major determinants of the year to year fluctuations of short-lived
species (Table 3, Fig.6). Thus a standardized analysis of trends and
fluctuations can help both the examination and quantification of
suggested relationships. It has been repeatedly emphasized (e.g., Austin
1981; Likens 1989) that only long-term vegetation studies will be
suitable for such purposes.

References

Austin, M.P. 1976. On non-linear species response models in ordination. Vegetatio 33: 33-41.

Austin, M.P. 1981. Permanent quadrats: An interface for theory and practice. Vegetatio 46: 1-10.

Austin, M.P. 1990. Community theory and competition in vegetation. In: Grace, J.B., & Tilman, D. (eds.) Perspectives on Plant Competition, pp. 215-238. Academic Press, San Diego.

Austin, M.P., Cunningham, R.B. & Fleming, P.M. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. Vegetatio 55: 11-27.

Bakker, J.P. 1989. Nature Management by Grazing and Cutting. Kluwer Academic Publishers, Dordrecht.

Bazzaz, F.A. 1987. Experimental studies on the evolution of niche in successional plant populations. In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds.) Colonization, Succession and Stability, pp. 245-272. Blackwell Scientific Publications, Oxford.

Besag, J. & Clifford, P. 1989. Generalized Monte Carlo significance tests. Biometrika 76: 633-642.

Box, G.E.P. & Jenkins, G.M. 1976. Time series analysis, forecasting and control. Revised edition. Holden-Day, San Francisco.

Cashen, R.O. 1947. The influence of rainfall on the yield and botanical composition of permanent grass at Rothamsted. J. Agricult. Sci., Cambridge 37: 1-10.

Chatfield, C. 1989. The Analysis of Time Series: An Introduction. Fourth Edition. Chapman and Hall, London.

Clifford, P., Richardson, S. & Hémon, D. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45: 123-134.

Collins, S.L., Bradford, J.A. & Sims, P.L. 1987. Succession and fluctuation in Artemisia dominated grassland. Vegetatio 73: 89-99.

Conway, G.R., Glass, N.R. & Wilcox, J.C. 1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51: 503-507.

Cramer, W. & Hytteborn, H. 1987. The separation of fluctuation and long-term change in vegetation dynamics of a rising sea shore. Vegetatio 69: 157-168.

de Leeuw, J., Olff, H. & Bakker, J.P. 1990. Year to year variation in peak above-ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. Aquat. Bot. 36: 139-151.

Dixon, W.J. (ed.) 1985. BMDP Statistical Software. University of California Press, Berkeley.

El-Shaarawi, A.H. & Damsleth, E. 1988. Parametric and nonparametric tests for dependent data. Water Resources Bulletin 24: 513-519.

Fresco, L.F.M. 1991. VEGROW: Processing of Vegetation Data. Shorthand manual v.4.0. S-BEES, Haren.

Gauch, H.G. & Whittaker, R.H. 1972. Coenocline simulation. Ecology 53: 446-451.

Hunt, R., Hope-Simpson, J.F. & Snape, J.B. 1985. Growth of the Dune Wintergreen (*Pyrola rotundifolia ssp. maritima*) at Braunton Burrows in relation to weather factors. Int. J. Biometeor. 29: 323-334.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211.

Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. 1987. Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen.

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press, Princeton.

Likens, G.E. 1989. Long-Term Studies in Ecology: Approaches and Alternatives. Springer-Verlag, New York.

Marquardt, D.W. 1963. An algorithm for least-squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 11: 431-441.

McCullagh, P. & Nelder, J.A. 1989. Generalized Linear Models. Second edition. Chapman & Hall, London.

Miller Jr., R.G. 1986. Beyond ANOVA, Basics of Applied Statistics. John Wiley & Sons, New York.

Olff, H. 1992. Effects of light and nutrient availability on dry matter and N allocation in six successional grassland species: Testing for resource ratio effects. Oecologia 89: 412-421.

Olff, H., Bakker, J.P. & Fresco, L.F.M. 1988. The effect of fluctuations in tidal inundation frequency on a salt-marsh vegetation. Vegetatio 78: 13-19.

Olff, H. & Bakker, J.P. 1991. Long-term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. J. Appl. Ecol. 28: 1040-1052.

Olff, H., Huisman, J. & van Tooren, B.F. submitted manuscript. Primary succession in coastal sand dunes: Species dynamics in relation to biomass and nutrient accumulation.

Penman, H.L. 1948. Natural evaporation from open water, bare soil and grass. Proc. Royal Soc. London, Series A 193: 120-145.

Pitt, M.D. & Heady, H.F. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. Ecology 59: 336-350.

SAS. 1988. SAS Language Guide for Personal Computers. Release 6.03 Edition. SAS Institute Inc., Cary NC.

Schat, H. 1982. On the ecology of some Dutch dune slack plants. PhD thesis, Free University Amsterdam.

Snow, A.A. & Vince, S.W. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. J. Ecol. 72: 669-684.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. Second Edition. Freeman, San Francisco.

SPSS. 1990. SPSS Advanced Statistics User's Guide (4.0). SPSS Inc., Chicago.

Talbot, M.W., Biswell, H.H. & Hormay, A.L. 1939. Fluctuations in the annual vegetation of California. Ecology 20: 394-402.

ter Braak, C.J.F. 1992. Permutation versus bootstrap significance tests in multiple regression and ANOVA. In: Jöckel, K.H., Rothe, G. & Sendler, W. (eds.) Bootstrapping and related techniques, pp. 79-86. Springer Verlag, Berlin.

ter Braak, C.J.F. & Looman, C.W.N. 1986. Weighted averaging, logistic regression and the Gaussian response model. Vegetatio 65: 3-11.

ter Braak, C.J.F. & Prentice, I.C. 1988. A theory of gradient analysis. Adv. Ecol. Res. 18: 272-317.

van Dam, D., van Dobben, H.F., ter Braak, C.J.F. & de Wit, T. 1986. Air pollution as a possible cause for the decline of some phanerogamic species in The Netherlands. Vegetatio 65: 47-52.

van der Maarel, E. 1981. Fluctuations in a coastal dune grassland due to fluctuations in rainfall: experimental evidence. Vegetatio 47: 259-265.

van der Meijden, R., Weeda, E.J., Holverda, W.J. & Hovenkamp, P.H. 1990. Heukels' Flora van Nederland. 21th edition. Wolters-Noordhoff, Groningen.

van Tooren, B.F., Schat, H. & ter Borg, S.J. 1983. Succession and fluctuation in the vegetation of a Dutch beach plain. Vegetatio 53: 139-151.

Watt, A.S. 1960. Population changes in acidiphilous grass-heath in Breckland, 1936-57. J. Ecol. 48: 605-629.

Yee, T.W. & Mitchell, N.D. 1991. Generalized additive models in plant ecology. J. Veg. Sci. 2: 587-602.