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Numerical assessment of plant species as indicators of the groundwater regime

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Abstract. The relation between the occurrence of plant species in environments varying in moisture status and groundwater regime was tested using numerical methods. The groundwater regime during the vegetation period was expressed by means of four parameters, the average (AVG), mean highest (HIGH), mean lowest (LOW) groundwater level and the maximum fluctuation (AMP). 67 records of five vegetation types were selected from hydrologically stable sites in brook valleys in the northern part of The Netherlands. Response curves were calculated for 30 representative species. Calculated optima for AVG, HIGH and LOW are strongly correlated to each other. The vegetation reacts independently from overall wetness to the amount of fluctuation of the groundwater level (AMP).

Response curves of single species as well as combinations of both present and absent species were used to find the best set of indicators for each parameter. The use of combinations of species clearly improves the indicating value of vegetation records. The vegetation appears to be the most sensitive to the parameter HIGH, which can thus be considered to be a key factor in controlling vegetation composition. The four parameters can be predicted satisfactorily only in the middle part of the investigated gradient. This is not only due to arithmetic artifacts, inherent to the applied method, but also to the fact that at average groundwater levels below – 60 cm or above 0 cm other factors become predominant.

Keywords: Calibration; Groundwater level; Marsh; Response analysis; Wet meadow.

Nomenclature: van der Meijden et al. (1990) for vascular plants; Westhoff & den Held (1969) for plant communities.

Introduction

In marshes and wet meadows a close relationship exists between groundwater regime and plant species composition (e.g. Tüxen 1954; Niemann 1963, 1973; Tüxen & Grootjans 1978; Klötzli 1969; Both & van Wirdum 1979; Grootjans & ten Klooster 1980; Egloff & Naf 1982; Schipper & Grootjans 1986; van Diggelen et al. 1996). Groundwater levels not only regulate the water supply, but also the availability of nutrients (Kemmers 1986; Verhoeven et al. 1993). The species composition in wetlands reflects a long term influence of the groundwater regime since most marsh plants reproduce mainly vegetatively. It may take a long time before disturbances in the groundwater regime have a full effect on plant species composition (Ellenberg 1952). Research into the indicator value of plant species on the groundwater regime should therefore be carried out in hydrologically stable sites.

Moisture indicator values for plant species have been published by Ellenberg (1979), Kleinke et al. (1974) and Landolt (1973). Indicator species are often used in landscape ecological studies to interpret hydrological conditions from vegetation data (Everts et al. 1988; van Diggelen et al. 1991b; Grootjans et al. 1993; ter Braak & Wiertz 1994). A reverse approach is to predict vegetation patterns from the output of quantitative hydrological models, using the relationship between groundwater level and vegetation as an intermediate (van Diggelen et al. 1991a; Noest 1994). The reliability of these techniques depends on the accuracy of the data applied. The demand for more exact and quantitative data on plant species response to groundwater level regime is, therefore, growing.

The groundwater level of a site is not a constant factor. It is the pattern of fluctuation which is important for plant growth. This pattern can be expressed by a variety of parameters which all may have different ecological consequences. Different authors use different parameters in describing the relationship between the occurrence of plant species and the groundwater regime. Niemann (1973) suggests four ecologically important parameters: average groundwater level, mean lowest level, mean highest level and median level. Noest (1994) used 16 parameters, including some describing the inundation duration and frequency. Scholle & Schrautzer (1993) simplify the groundwater regime to only three parameters: mean level, an index for the fluctuation pattern and duration of flooding, although without testing the validity of this simplification. It is still unclear which of all the possible parameters that can be calculated from a series of measurements are the most important for the distribution of marsh plants. A number of these parameters are likely to be closely correlated with each other.

Another matter is whether single plant species or vegetation types can best be used as indicators (Zonneveld 1988). Species have the advantage that their spatial distribution is clearly defined. On the other hand, they can have a wide ecological tolerance and are sometimes able to survive a long time after the optimal conditions for their presence have changed. Vegetation types, defined below the level of subassociations, however, often have very narrow ecological tolerances (Tüxen 1954; Niemann 1973). They also have the advantage that the absence of some species can be of significant value. The use of species absences indicating environmental conditions has, in general, been disregarded (ter Braak & Looman 1986). The occurrence of a species in the absence of a second species can render more precise indications.

A disadvantage of the use of vegetation types as indicators is that, with increasing human pressure on the landscape, the plant communities tend to loose their characteristic and differentiating species. The assignment of individual vegetation stands to a well defined vegetation type then becomes difficult and biased. A solution could be to use species combinations. Those are both well-defined and can be expected to have much narrower response curves, which could make them more accurate indicators than single species.

The present study aims to answer the following questions: 1. Which are the main groundwater regime parameters controlling vegetation composition in wet to moist environments? 2. How accurate can those parameters be indicated by combinations of present and absent plant species?

Methods

Vegetation data

The data used for the assessment of indicators were acquired in stream valleys in the northern part of The Netherlands. This area is presumed to be small and homogeneous enough to prevent plant-groundwater relationships from being influenced by climatological or geological factors. From several studies, which took place over the period 1976-1987, a careful selection was made on the basis of the hydrological stability of the sampled sites. A site was assumed to be hydrologically constant (the vegetation reflecting the groundwater regime) when there were no clear historical or ecological signs of disturbance such as desiccation, acidification or eutrophication. All vegetation recordings are from semi-natural grasslands on peat soils under extensive management (mown annually, no grazing, no fertilisation). The plant communities under consideration can be classified as *Lolio-Potentillion anserinae*, *Arrhenatherion elatioris*, *Calthion palustris*, *Magnocaricion elatae* and *Caricion curto-nigrae*.

67 records from plots of 2 m × 2 m were used. For the response analysis 30 species were selected on the basis of the following criteria:

(1) characteristic of one of the discerned vegetation types;
(2) present in at least four vegetation records;
(3) represented in the entire set of vegetation types under consideration.

Extra species were chosen with a distribution over a wider range of vegetation types. It was necessary to have more indicating species present in each vegetation record. Although these species, in general, will have a wider tolerance for groundwater variables, their combination with other species can improve the indicating value of the whole set.

Hydrological data

Groundwater levels were measured at least once, but mostly twice a month, between March 15 and October 20 (vegetation period). Filter depths varied from 80 to 120 cm below the surface.
The following parameters were calculated:

(1) The average water table during the vegetation period (taking the temporal distribution of observations into account) (**AVG**);
(2) The arithmetic mean of the three highest groundwater levels observed (**HIGH**);
(3) The arithmetic mean of the three lowest groundwater levels observed (**LOW**);
(4) The amplitude of the groundwater level = HIGH-LOW (**AMPL)**.

The calculation of indicator values

Indicator values were calculated using the ecological response model presented by Huisman et al. (1993). The indicator values are the optimum values of logit response curves (the value of the environmental factor, where the species has a maximum probability of occurrence). The type of curve is selected by a stepwise sequence, from a horizontal line via monotonously increasing or decreasing towards a (skewed) Gaussian curve.

The most obvious and most widely spread index to be used as an indicator value is the weighted average (ter Braak & Barendregt 1986). An alternative index is the maximum likelihood estimate, which – for reasons of consistency with respect to the model- is used in this paper. In practice, the results obtained by these two measures do not differ much, at least if the curve is not extremely skewed.

The tolerance of the species with respect to the factors is expressed as:

$$\text{Width} = P_s / P_m \quad (1)$$

where P_s is the fraction of the total surface which is occupied by the surface below the curve and P_m is the maximum probability of occurrence. The software used for these calculations was SPSS-PC+ (Anon. 1990), VEGROW (Fresco 1991) and ad-hoc programs.

Calibration

From the selected 30 indicator species a large number of significant indicator combinations can be derived. It is obvious that indicator combinations with a narrow ecological amplitude (tolerance) with respect to the factor render a more reliable estimation, but only using those has a disadvantage: a large number of indicator combinations is needed to cover an environmental gradient. If the overlap of the indicators is small, the application of the results of any calibration technique is vulnerable to many kinds of errors. It has the additional disadvantage of a large probability of sites containing only one or even no indicators. An appropriate set from all available significant indicator combinations needs to be selected optimizing both the number of used indicators (should be low) and the accuracy of the predictions for as many of the sites as possible.

Responses of combinations of present (positive) and absent (negative) species were calculated and tested using the same technique as that for single species. In the calibration procedure the indicated value of a site is calculated as the average of the (significant) indicator values of the species (combinations) present. For all sites the indicated values are then compared to the measured values and the correlation coefficient (r^2 = residual sum of squares explained by correlation over total sum of squares) is calculated.

The following procedure was applied:

1. All significant indicator combinations are calculated in six sets:
   A. Only one species
   B. Two positive species
   C. Three positive species
   D. One positive and one negative species
   E. Two positive and one negative species
   F. All combinations A-E together

2. Largely overlapping indicator combinations are removed (the ad-hoc computer program shows lists of overlapping combinations; the user decides which combinations will be used).
3. The relationship between observed values of the factor and values calculated using all the remaining combinations is expressed as r^2_N (N combinations will be used).
4. For each combination C_i a value r^2_{N-i} is calculated, expressing the fit between observed and calculated values for all remaining indicators after removal of C_i. The combination for which the value $[r^2_N - r^2_{N-i}]$ is minimal is removed from the list; N gets the value $N - 1$. This is repeated until $[r^2_N - r^2_{N-i}]$ is statistically significant (Huisman et al. 1993). To prevent a large number of sites not containing enough indicator combinations, a second criterion is used: if more than 5 % of the sites have less than two indicators, the removal is cancelled.
5. Finally a linear rescaling was completed as follows:

$$\text{if } V_c = b \cdot V_o + a \text{ then } V'_c = \frac{V_c - a}{b} \quad (2)$$

where V_o are the observed values and V_c are the calculated values.

Results

The response analysis

Table 1 shows the results of the response analysis of the 30 species with respect to the four hydrological factors. Species are grouped according to the syntaxa which they represent.

The species belonging to the tall sedge community *Magnocaricion* occupy the wettest places. This vegetation type is inundated even in the vegetation period (optimal mean highest level is between 0 and +10 cm). The optimal average level is between – 10 cm and +10 cm, while lowest groundwater levels during the vegetation period do not exceed – 30 cm. The optimum amplitude varies from 15 cm to 48 cm, where the characteristic species of this group have a low amplitude and the eutrophic grasses have a high optimal amplitude.

The next group of species belongs to the *Caricion curto-nigrae*, a small sedge community of very wet sites. The optimum average level is around – 25 cm, while the optimum mean highest level lies between 0 and – 5 cm. The optimum value for the amplitude lies around 30 cm. Only *Carex rostrata* seems to prefer much wetter sites, although these values have been derived from monotonously increasing curves. This signifies that probably only a part of the gradient has been sampled. It is then impossible to distinguish the optimum value near the limit of the gradient.

The species of the *Calthion palustris* differ con-

Table 1. Response curves of 30 species on four ground water variables. Opt = Optimum (indicator-) value; Wid = width of the curve (see text); Significance: * $p < 0.0500$; ** $p < 0.0050$; ***$p < 0.0005$; n.s. = non-significant; M = monotonously increasing or decreasing curves.

	Average level		Highest level		Lowest level		Amplitude	
	Opt.	Wid	Opt.	Wid	Opt.	Wid	Opt.	Wid
Magno-Caricion								
Phalaris arundinacea	**+ 4**	0.26 ***	**+ 30**	0.16 *** M	**– 29**	0.24 n.s.	**48**	0.37 ***
Carex acuta	**+ 10**	0.14 **	**+ 12**	0.16 *	**– 31**	0.24 *	**11**	0.11 n.s.
Carex aquatilis	**– 2**	0.28 ***	**+ 5**	0.35 ***	**– 20**	0.29 **	**14**	0.28 **
Glyceria maxima	**– 9**	0.30 **	**– 1**	0.79 *	**– 30**	0.38 **	**42**	0.18 n.s.
Caricion curto-nigrae								
Carex rostrata	**– 10**	0.18 n.s.	**+ 30**	0.03 *** M	**+ 6**	0.22 ** M	**20**	0.34 ***
Ranunculus flammula	**– 14**	0.29 n.s.	**+ 2**	0.40 ***	**– 43**	0.26 n.s.	**46**	0.38 ***
Hydrocotile vulgaris	**– 23**	0.30 **	**– 5**	0.35 ***	**– 38**	0.21 n.s.	**28**	0.27 ***
Eleocharis palustris	**+ 3**	0.21 n.s.	**– 5**	0.03 n.s.	**– 31**	0.24 n.s.	**40**	0.24 ***
Viola palustris	**– 28**	0.31 ***	**– 5**	0.18 **	**– 48**	0.39 ***	**28**	0.17 n.s.
Calthion palustris								
Senecio aquaticus	**+ 10**	0.24 *** M	**+ 30**	0.09 *** M	**+ 6**	0.18 *** M	**34**	0.20 **
Caltha palustris	**– 17**	0.57 ***	**– 3**	0.58 ***	**– 32**	0.56 ***	**31**	0.55 ***
Carex acutiformis	**– 15**	0.25 n.s.	**– 4**	0.39 n.s.	**– 30**	0.30 n.s.	**16**	0.30 *
Myosotis palustris	**– 38**	0.79 n.s.	**– 5**	0.76 ***	**– 30**	0.52 n.s.	**100**	0.83 n.s.
Lychnis flos-cuculi	**– 45**	0.84 n.s.	**– 9**	0.46 n.s.	**– 33**	0.41 n.s.	**55**	0.60 n.s.
Lotus uliginosus	**– 32**	0.43 **	**– 9**	0.28 **	**– 85**	0.38 n.s.	**20**	0.35 **
Filipendula ulmaria	**– 39**	0.55 *	**– 14**	0.83 *	**– 43**	0.76 *	**100**	0.55 n.s.
Lolio-Potentillion anserinae								
Glyceria fluitans	**– 23**	0.23 **	**– 9**	0.38 **	**– 52**	0.21 *	**21**	0.36 ***
Alopecurus geniculatus	**– 46**	0.40 **	**– 15**	0.40 ***	**– 85**	0.46 **	**48**	0.41 *
Arrhenaterion elatioris								
Cynosurus cristatus	**– 28**	0.26 **	**– 14**	0.43 ***	**– 57**	0.26 n.s.	**35**	0.25 *
Veronica chamaedris	**– 41**	0.32 ***	**– 26**	0.26 **	**– 99**	3.26 *	**55**	0.20 *
Remaining species								
Mentha aquatica	**– 14**	0.29 **	**– 3**	0.55 n.s.	**– 35**	0.30 n.s.	**15**	0.59 n.s.
Equisetum fluviatile	**– 14**	0.55 ***	**– 6**	0.63 ***	**– 39**	0.74 **	**23**	0.38 **
Carex panicea	**– 35**	0.44 ***	**– 9**	0.35 ***	**– 64**	0.44 ***	**38**	0.25 *
Cirsium palustre	**– 49**	0.61 n.s.	**– 10**	0.37 ***	**– 41**	0.55 n.s.	**100**	0.64 n.s.
Anthoxanthum odoratum	**– 30**	0.23 n.s.	**– 10**	0.19 n.s.	**– 50**	0.20 n.s.	**52**	0.79 *
Stellaria uliginosa	**– 22**	0.28 n.s.	**– 12**	0.32 ***	**– 40**	0.27 n.s.	**30**	0.33 *
Poa pratensis	**– 56**	0.51 n.s.	**– 15**	0.39 ***	**– 69**	0.53 n.s.	**100**	0.64 n.s.
Plantago lanceolata	**– 43**	0.54 *	**– 59**	0.65 * M	**– 65**	0.51 ***	**39**	0.25 n.s.
Holcus lanatus	**– 84**	0.57 n.s.	**– 59**	0.49 ** M	**– 125**	0.61 n.s.	**2**	0.43 * M
Ranunculus repens	**– 84**	0.52 * M	**– 59**	0.94 n.s.	**– 125**	0.45 n.s.	**2**	0.33 n.s.
Total significant indicators	**19**		**24**		**14**		**19**	

siderably in their optima. Optima for the average level vary from – 40 cm to 0, while optima for amplitude, mean high and mean low show even larger variations. This vegetation type has a broad range of subtypes from quite different environments. The optima for the characteristic species of the *Calthion palustris* – *Caltha palustris*, *Lychnis flos-cuculi*, *Myosotis palustris*, *Lotus uliginosus* – are relatively close to each other (optimum average level is – 17 cm, with an optimum amplitude of around – 30 cm). An exception is *Senecio aquaticus* which clearly prefers wetter sites. These values stem again from monotonously increasing response curves. Normally, this vegetation type is not flooded during the growing season (optimum high level is about – 5 cm). The species which differ considerably in their optima are the species representing subassociations of the *Calthion palustris*: *Carex aquatilis*, *Carex acutiformis*, *Filipendula ulmaria* and *Carex panicea*.

The species from the highly productive, not too wet grassland communities *Lolio-Potentillion anserinae* and *Arrhenaterion elatioris* have the lowest optima. This is also true for the species in the remaining group which frequently occur in these grasslands such as *Plantago lanceolata* and *Poa pratensis*. The significant optima are often wide, indicating a large tolerance. Indeed, the species in these groups are commonly found in a broad range of other vegetation types. These species are not very responsive to groundwater level parameters. Optima are in the region of – 40 cm to – 80 cm for the average level with an amplitude of ca. 45 cm to 55 cm.

Correlation between the groundwater level variables

Correlations between the groundwater level variables are presented in Table 2. The bottom left part shows the coefficients between the measured values per site ($N = 67$). In the top right of the table the correlations between the calculated optima per species ($N = 30$) are given.

Measured values, as well as calculated optima, show

Table 2. Correlation coefficients between measured values for groundwater parameters per site ($N = 67$) (bottom left) and calculated optimum values per species ($N = 30$) (top right). Significance: * = $p < 0.05$; ** = $p < 0.005$.

	AVG	HIGH	LOW	AMP	
AVG	—	+ 0.829**	+0.824**	– 0.235 ns	
HIGH	+ 0.878**	—	+0.835**	+ 0.188 ns	N = 30
LOW	+ 0.734**	+ 0.623**	—	+ 0.036 ns	
AMP	– 0.508**	– 0.123 ns	– 0.791**	—	
		N = 67			

a strong positive correlation between the average groundwater level and both highest and lowest levels. This means that when a site has a high average groundwater level, the lowest and highest levels are also expected to be high and *vice versa*. Plant species which prefer a high average level also depend on high highest and lowest levels, especially as these correlations between calculated optima are strong.

The situation is different for the correlation between the amplitude and the other three parameters. Highly negative correlations between AMP and both AVG and LOW were found in the measured values. The correlation between LOW and AMP is the most negative, while the correlation between HIGH and AMP is insignificant. This means that AMP is predominantly regulated by the lowest groundwater table during the vegetation period. Such a negative correlation between LOW and AMP is absent for the calculated optima. This shows that the species investigated can react to the fluctuation of the water table (AMP) independent of the average wetness of the soil (as indicated by AVG, HIGH and LOW together). This is nicely illustrated by *Carex aquatilis* and *Phalaris arundinacea*, both having the same optimum for AVG, but different optima for AMP.

Indication of groundwater regime parameters

For all four parameters it was found that they are better indicated by combinations of species than by single species alone (Table 3). Method F, in which all types combinations are used, gives the best results. The correlation between actual and indicated values is the best for all parameters. Compared to using only one type of combination, far less indicator combinations are needed. This trend is less clear, though, for the highest groundwater level, which is indicated quite well by

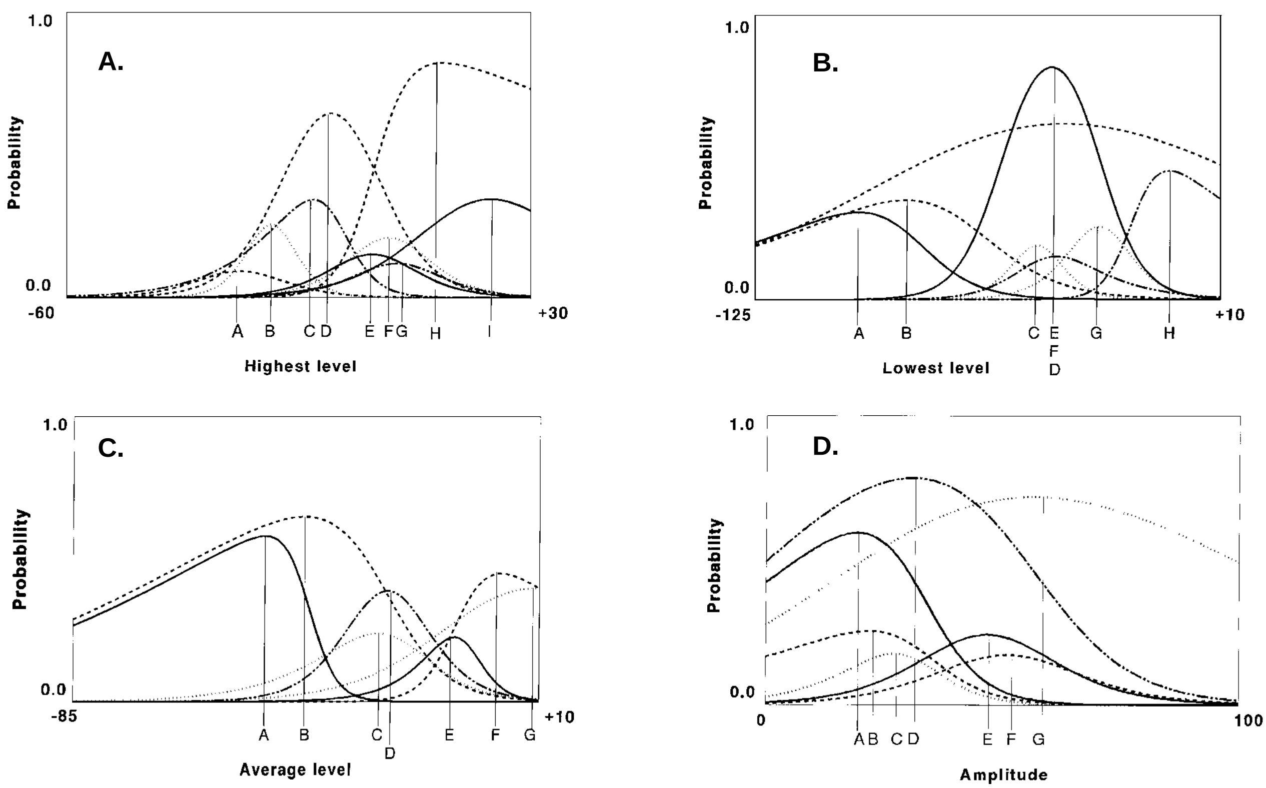

Fig. 1.A. Response curves of nine indicators for 'highest level'. For codes A-I, see App. 1B). **B.** Response curves of eight indicators for 'lowest level'. For codes A-H: see App. 1C. **C.** Response curves of seven indicators for 'average level'. For codes A-G, see App. 1A. **D.** Response curves of seven indicators for 'amplitude'. For codes A-G, see App. 1D.

Table 3. Precision of indication for the six different types of combinations (A-F). + = one present species in indicator combination; - = one species absent in indicator combination.

Method	Correlation *r*				Nr. of combinations needed				Nr. of sites estimated				Mean residue(cm)			
	AVG	HIGH	LOW	AMP	AVG	HIGH	LOW	AMP	AVG	HIGH	LOW	AMP	AVG	HIGH	LOW	AMP
A (+)	0.72	0.76	0.60	0.74	16	17	12	17	67	66	67	65	14.0	8.9	20.1	9.4
B (++)	0.73	0.81	0.63	0.75	19	22	17	24	67	66	67	65	10.1	8.3	20.5	8.5
C (+++)	0.74	0.83	0.62	0.88	31	23	26	15	67	66	67	52	15.2	8.4	24.3	3.7
D (+-)	0.74	0.77	0.67	0.69	40	33	24	11	67	64	67	53	13.4	9.3	18.5	5.0
E (++-)	0.74	0.77	0.67	0.88	44	34	32	13	67	64	67	52	16.8	9.6	18.1	4.3
F (all)	0.83	0.86	0.71	0.80	14	28	8	7	67	66	67	67	12.4	8.3	20.0	8.3

single species only. Table 3 also shows that adding the absence of species does not necessarily improve the indicating results (method B-D and C-E compared).

The selected indicator combinations with the indicator values and the rescaling equations are given in App. 1A-D. The number of combinations needed to comprise the entire gradient is small for the parameters LOW and AMP, higher for AVG and higher still for HIGH. As the indicator combinations are selected in such a way that they exclude each other as much as possible, the indicators for LOW and AMP are more frequently occurring than those for HIGH and AVG. However, a lower number of indicator combinations implies a worse correlation between observed and estimated values. The selected species seem to be the most sensitive to the mean highest groundwater level during the vegetation period. This is in accordance with Table 1, which shows the highest groundwater level having the most significant single species indicators (24 out of 30 species).

Fig. 1 A-D shows a large variation in both tolerance and maximum probability among the indicator combinations. For the groundwater parameters representing the 'wetness' of the profile (AVG, LOW and HIGH), the maximum probability generally is the highest in the middle of the gradient. At the same time, the tolerance in this part of the gradient is low. At both ends of the gradient the indicating value of the species present is weaker, especially at the dry side of the gradient. The best indicator species for the groundwater regime are found at a mean groundwater level between 0 and – 50 cm.

The indicator species and species combinations for the amplitude (Fig. 1D) cover the middle part of the gradient only. Both high (> 60 cm) and low (< 20 cm) amplitudes are not indicated by this set of species.

The groundwater regime can be predicted fairly well over most of the gradient. The estimated values have the best fit with the observed values in the middle part (Fig. 2 A-D). Towards the extremes of the gradient predictions become inaccurate, especially on the dry side. Mean water table during the growing season can be predicted with an accuracy of ca. 4 cm for that part of the gradient that has mean water tables higher than – 60 cm.

Discussion

Two main factors, linked to the groundwater regime, appear to control the occurrence of marsh and wet meadow plant species. The first factor is the general wetness of a site, represented by mean, highest and lowest groundwater level, which are strongly correlated with each other. The second factor is the fluctuation of the groundwater level of a site. This factor is negatively correlated with the other three parameters, especially the lowest water table.

The high positive correlations between the parameters representing the wetness of a site do not imply that the different species react in the same way to these three parameters. The trend is clear (species with a high optimum for mean groundwater level also grow at sites with high HIGH and high LOW levels), but from the response analysis it can be seen that a species can have a clearly significant optimum, for example for the mean highest level and no significant optima for both AVG and LOW (for instance *Cirsium palustre* and *Ranunculus flammula*).

Plant species seem to respond independently to the amplitude of the water table. There is no correlation between 'wetness' and 'fluctuation' in the calculated optima for the species. The occurrence of a species is determined by both the average wetness of the soil and the degree of fluctuation of the water table, independently from each other. This conclusion is based on only four of the many other possible parameters of the groundwater regime having been considered. These four parameters are commonly considered to be the most important. Inundation, which is also thought to be ecologically important, is not treated as a separate parameter. Only inundation during the vegetation period, which is the most important inundation period (Noest 1993), is implicit in the parameter HIGH. Therefore, it is probable that adding extra parameters to this set will not change the overall conclusion.

This study shows that a set of indicators for a given environmental factor supplies sufficiently accurate estimations only in the middle part of the gradient from

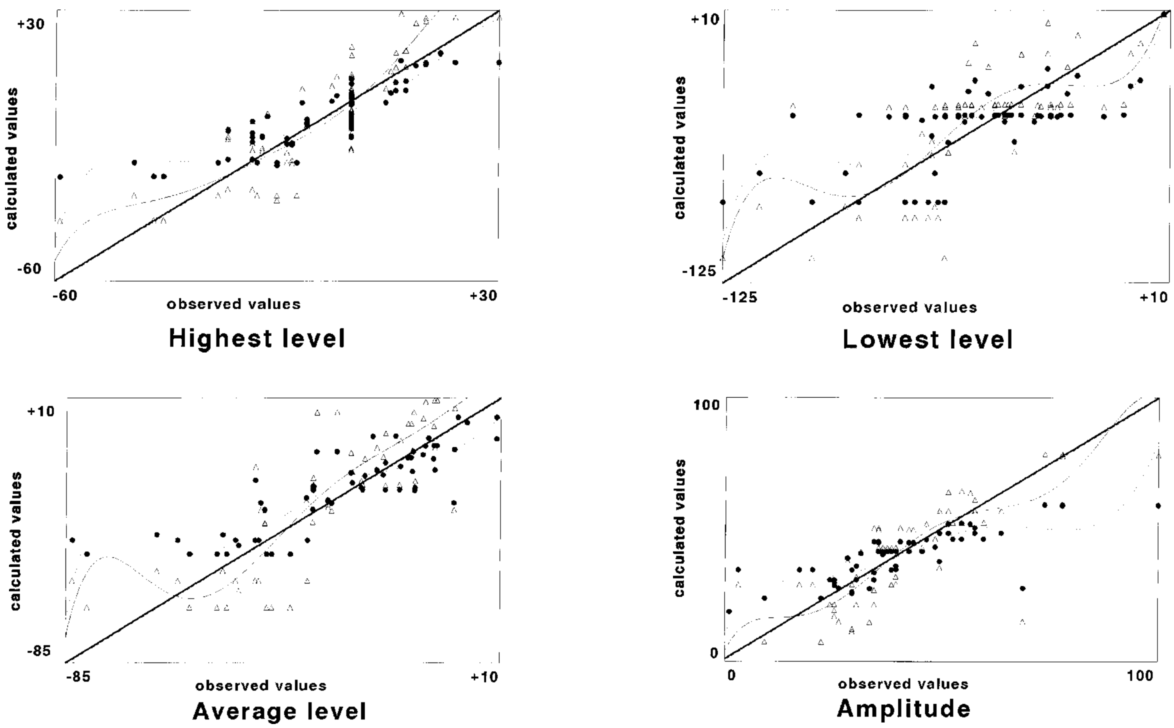

Fig. 2. Estimated values plotted against observed values for each of the parameters. Before (triangles) and after (dots) rescaling. Through both sets of estimations a 5th degree parameter was fitted for the purpose of better comparison (dotted line: not rescaled; striped/dotted line: rescaled).

which the indicators were taken. At first we meet an arithmetic artefact: no indicator values outside the measured gradient are present, hence the occurrence of a combination which indicates a too low or a too high value can never be compensated by the presence of another combination. This causes a ‘shrinking’ of the gradient. The applied rescaling only corrects this partially. Furthermore, the response curves of (combinations of) species presented here show a wider tolerance and a smaller probability of occurrence at the extremes of the range (especially the dry end). Apparently, the groundwater regime becomes less important as a factor controlling vegetation composition in this range.

A larger number of species or species combinations is needed to predict the highest water table than the average or lowest water table. The consequence is that HIGH is predicted more accurately than the other parameters. It means that the selected species are more sensitive for HIGH than for the other parameters. This confirms the conclusion that the mean high groundwater level during the vegetation period is a key factor controlling the vegetation distribution. This parameter comprises inundation during the vegetation period, which Noest (1994) found to be a main ecological factor.

On the basis of this data set the highest groundwater levels can be predicted quite accurately between values of – 40 cm and + 10 cm to the surface. On the wetter part of the gradient predictions could be improved by adding extra data to the data set. More data could be added from stands with peat forming mires, for example from the *Caricion lasiocarpae* and *Phragmition australis*.

Amplitudes are predicted well between values of 20 and 60 cm. When the amplitude of the groundwater table reaches 60 cm, the actual value of the amplitude becomes apparently less important. The water holding capacity of the subsoil can enhance or dampen the effects of a strongly fluctuating water table. For the predictions of low amplitudes it could again be that the addition of data from permanently wet sites might improve the results, as these are not represented in this data set.

For the wettest part of these gradients it is generally accepted that water quality has a major impact on the species composition (Wilcox et al. 1986; Wassen et al. 1989; Barendregt 1993). These vegetation types exist only under the condition of a permanent high water table. The water quality differentiates in this very wet environment. This means that a number of good indicator species can probably be found in this part of the gradient, but it also means that predictions of vegetation development will be useless without taking into account the water chemistry.

The results presented here are based on data from various years, including both wet and dry years. Since groundwater levels vary from year to year, depending on climatological differences, a certain amount of noise is included in the data and, therefore, in the results. For groundwater-fed vegetation types this variation over the years will be small, as the supply of groundwater buffers the groundwater levels in dry periods. The addition of extra data will make the results more representative for an average hydrological year. Apart from the fact that data on groundwater levels in hydrologically stable sites are very difficult to find, care should be taken that these extra data are spread homogeneously over wet, dry and average years. If this is not the case (as it often is with data from the past) an alternative is to calculate groundwater levels for a site as they would have been in a 'normal' hydrological year, using a simple 1-dimensional model for water transport in the upper soil layer. This would greatly reduce the amount of data needed, although an extra error in the data is introduced, which is difficult to estimate.

The applied method delivers a set of good indicator combinations for the groundwater regime. One should, however, realize that certain combinations of species may exist only temporarily at sites where recent changes in hydrology have occurred (unequal delay during succession). This will often be the case in northwestern Europe. Furthermore, the indicated values by a certain indicator combination is geographically limited. One should be careful with the extrapolation to other areas. Only by adding extra data from these areas can results be expected to be reliable.

It may be concluded that vegetation distribution is mainly determined by the highest water table and the fluctuation of the water table during the vegetation period. The prediction of future vegetation distribution from hydrological model outputs primarily needs to consider these two factors, at least for the not too wet (AVG < 0 cm) and not too dry (AVG > – 60 cm) vegetation types.

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For App. 1, see next page.

App. 1. a. Indicator species combinations for average level. Corr. 0.830, no. of sites estimated 67. Rescaling: E' = – 24.767 + 1.129E. **b**. Indicator species combinations for highest level. Corr. 0.855, no. of sites estimated 66. Rescaling: E' = 12.899 + 1.933E. **c**. Indicator species combinations for lowest level. Corr. 0.711, no. of sites estimated 67. Rescaling: E' = – 48.831 + 0.869E. **d**. Indicator species combinations for amplitude. Corr. 0.798, no. of sites estimated 67. Rescaling: E' = 40.540 + 1.492E. Indicator species combinations indicated with letters (see Fig. 1).

a.

+Alo gen	– 46	A	+Care act +Plan lan +Vero cha	– 20	
+Plan lan	– 43		+Ment aqu +Care act	– 7	E
+Fili ulm	– 39	B	+Calt pal +Stel uli	– 7	
+Glyc flu	– 23		+Calt pal –Anth odo	+ 0	
+Hydr vul	– 23	C	+Glyc max –Ment aqu	+ 1	F
+Calt pal +Lych flo –Ranu fla	– 22		+Calt pal +Ment aqu –Care pan	+ 5	
+Calt pal +Myos pal +Glyc max	–20	D	+Calt pal +Care aqu –Care acu	+ 8	G

b.

+Vero cha	– 25	A	+Care aqu –Glyc max	+ 2	
+Cyno cri –Ment aqu	– 25		+Care aqu +Myos pal –Phal aru	+ 3	
+Alop gen –Myos pal	– 22		+Care aqu +Myos pal –Sene aqu	+ 3	F
+Alop gen –Ment aqu	– 20	B	+Care aqu +Myos pal –Poa pra	+ 3	
+Calt pal –Care pan	– 14		+Calt pal +Care aqu –Ranu fla	+ 4	
+Plan lan +Calt pal –Eleo pal	– 14		+Ranu fla +Myos pal –Sene aqu	+ 4	G
+Lych flo +Myos pal –Sene aqu	– 13	C	+Care aqu +Myos pal –Care pan	+ 4	
+Calt pal +Anth odo +Plant lan	– 10	D	+Care aqu +Myos pal –Care ros	+ 4	
+Calt pal –Glyc max	– 7		+Care aqu –Ranu fla	+ 11	
+Ment aqu +Myos pal –Care acu	– 6		+Care aqu –Lych flo	+ 13	
+Calt pal +Care act –Care aqu	– 5		+Glyc max	+ 13	H
+Hydr vul	– 4		+Myos pal +Ranu fla	+ 15	
+Calt pal +Care act –Ranu fla	– 1		+Care acu	+ 16	
+Calt pal +Stel uli	+ 0	E	+Calt pal +Phal aru	+ 18	I

b.

+Vero cha	– 99	A
+Alop gen	– 85	B
+Viol pal –Calt pal	– 45	C
+Fili ulm	– 43	F
+Ment aqu +Glyc max –Sene aqu	– 42	D
+Calt pal –Care act	– 42	E
+Calt pal +Stel uli	– 27	G
+Calt pal +Ment aqu –Eleo pal	– 10	H

d.

+Lotu uli	20	A
+Glyc flu	21	B
+Hydr vul	27	C
+Calt pal	31	D
+Phal aru	48	E
+Holc lan +Alop gen	52	F
+Anth odo	52	G

Shortened species names:

Alopecurus geniculatus	Alop gen	*Eleocharis palustris*	Eleo pal	*Myosotis palustris*	Myos pal
Anthoxanthum odoratum	Anth odo	*Equisetum fluviatile*	Equi flu	*Phalaris arundinacea*	Phal aru
Caltha palustris	Calt pal	*Filipendula ulmaria*	Fili ulm	*Plantago lanceolata*	Plan lan
Carex acuta	Care acu	*Glyceria fluitans*	Glyc flu	*Poa pratensis*	Poa pra
Carex acutiformis	Care act	*Glyceria maxima*	Glyc max	*Ranunculus flammula*	Ranu fla
Carex aquatilis	Care aqu	*Holcus lanatus*	Holc lan	*Ranunculus repens*	Ranu rep
Carex panicea	Care pan	*Hydrocotyle vulgaris*	Hydr vul	*Senecio aquaticus*	Sene aqu
Carex rostrata	Care ros	*Lotus uliginosus*	Lotu uli	*Stellaria uliginosa*	Stel uli
Cirsium palustre	Cirs pal	*Lychnis flos-cuculi*	Lych flo	*Veronica chamaedris*	Vero cha
Cynosurus cristatus	Cyno cri	*Mentha aquatica*	Ment aqu	*Viola palustris*	Viol pal