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The need of data harmonization to derive robust empirical relationships between soil conditions and vegetation

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Abstract

Question: Is it possible to improve the general applicability and significance of empirical relationships between abiotic conditions and vegetation by harmonization of temporal data?
Location: The Netherlands.
Methods: Three datasets of vegetation, recorded after periods with different meteorological conditions, were used to analyze relationships between soil moisture regime (expressed by the mean spring groundwater level – MSL_t calculated for different periods) and vegetation (expressed by the mean indicator value for moisture regime F_m). For each relevé, measured groundwater levels were interpolated and extrapolated to daily values for the period 1970-2000 by means of an impulse-response model. Sigmoid regression lines between MSL_t and F_m were determined for each of the three datasets and for the combined dataset.
Results: A measurement period of three years resulted in significantly different relationships between F_m and MSL_t for the three datasets (F-test, $p < 0.05$). The three regression lines only coincided for the mean spring groundwater level computed over the period 1970-2000 ($MSL_{climate}$) and thus provided a general applicable relationship. Precipitation surplus prior to vegetation recordings strongly affected the relationships.
Conclusions: Harmonization of time series data (1) eliminates biased measurements, (2) results in generally applicable relationships between abiotic and vegetation characteristics and (3) increases the goodness of fit of these relationships. The presented harmonization procedure can be used to optimize many relationships between soil and vegetation characteristics.

Keywords: Delayed response; Groundwater level; Indicator Value; Time series analysis.

Abbreviations: F_m = mean indicator value for moisture regime; MSL = Mean spring groundwater level; $RMSE$ = Root mean squared error.

Introduction

A central question in ecology is how species and communities respond to variation in environmental conditions. In plant ecology, most studies focus on relationships between vegetation and measured site factors such as temperature, soil acidity, soil nutrient availability and groundwater level. These site factors act as drivers in selecting species with different physiological characteristics. Only plant species with the appropriate physiological characteristics can survive in specific environmental conditions. Numerous studies exist in which field measurements of soil and groundwater are used to define relationships between vegetation and site characteristics. Several researchers have focused on the response of plant species or vegetation types (Allen-Diaz 1991; Dzwonko 2001; Schröder et al. 2005), while others, in pursuit of relationships that are generally applicable, used plant traits (Cousins & Lindborg 2004; Kennedy et al. 2003; McGill et al. 2006) or indicator values (Diekmann 1995; Ertsen et al. 1998; Schaffers & Sýkora 2000) as response variables of vegetation. Empirical relationships derived from such studies have been applied for predictions (Guisan & Zimmermann 2000), for instance, to assess the effects on vegetation of water management (e.g. Witte et al. 1992), of vegetation management (e.g. Jansen & Roelofs 1996), of climate change (e.g. Thomas et al. 2004) and of air pollution (e.g. van Dobben & ter Braak 1999).

However, because of temporal fluctuations in site conditions in combination with delayed vegetation responses, the general applicability of these empirical relationships cannot be taken for granted. Usually, the implicit assumption of these studies is that plant species composition reflects site conditions over many years. Such equilibrium is assumed as sufficient knowledge on the temporal dynamics of plant species composition on changes in site conditions is lacking. Moreover, since there is no unambiguous rule for length and frequency of a measuring program needed to calculate representative site conditions, and since the time and money to perform a research are usually limited, researchers often base their relationships on short time series or even to single measurements.

There is much evidence that site factors that are important to plant performance (e.g. soil water content, nitrate, phosphate, total organic carbon) may vary considerably in time (between days as well as years) (Cain et al. 1999; Farley & Fitter 1999; Kieft et al. 1998). Single or short-term (both months and years) measurements, therefore, probably deviate from the site conditions that the species composition of the vegetation is assumed to reflect. As a consequence of this temporal variability in site factors, it is likely that differences occur among empirical relationships with the same scope, but based on different measurement periods.

In this paper, we will analyze differences between empirical relationships, caused by temporal variation in site conditions between measurement periods. We will discuss the effect of time series length, i.e. the number of years in which a site factor has been measured, on the general applicability and on the goodness of fit of relationships between site factors and vegetation characteristics.

As a case study, we will analyze empirical relationships between groundwater level, relative to soil surface, and moisture indicator values *sensu* Runhaar (Witte et al. 2007). Empirical relationships between the mean groundwater level in spring (*MSL*) and moisture indicator values (F_m) are commonly used in ecological modelling. Therefore, we decided to use *MSL* as the variable to be correlated with F_m.

Groundwater levels vary within and between years through variability in meteorological conditions and particularly through variability in precipitation surplus. Therefore, it is hypothesized that empirical relationships between *MSL* and moisture indicator values as determined for short time series depend on the prevailing meteorological conditions. We will investigate whether it is possible to minimize systematic differences between the empirical relationships, caused by temporal variation in meteorological conditions, by harmonization of groundwater level series measured in different periods. Harmonization is the minimization of systematic differences between different sources of environmental measures (Keune et al. 1991). Thus, the effect of temporal meteorological variation will be filtered out, improving the significance and general applicability of the relationships.

Methods

General approach

We used three datasets of vegetation relevés and observed groundwater levels in, or immediately next to, each relevé. Each dataset contained vegetation relevés taken in the same year, but different from the other two datasets. Groundwater levels were measured fortnightly and for a limited number of years (see below). To be able to analyze soil moisture conditions over long time series, the groundwater level time series were extended to the period 1970-2000, as well as interpolated to daily values.

For each relevé we calculated a mean indicator value for moisture regime, F_m, based on the indicator values of the individual plant species (see below). Then, for each dataset, F_m was regressed on MSL_t computed over a period of *t* years, preceding the vegetation record. We validated the statistical differences between the relationships for each of the datasets with emphasis on how the differences were influenced by time series length *t*. We quantified the need for data harmonization by cross-prediction. Additionally, we studied changes in the relationship between MSL_t and F_m with increasing *t* for all datasets merged into one database.

Data

The three datasets considered are: (A) the dataset of Runhaar (1989), with 188 relevés taken in 1987 and groundwater levels observed from 1980-1987; (B) the dataset of Ertsen (1999) with 56 relevés from 1991 and groundwater levels observed from 1991-1993 and (C) the dataset of the Dutch State Forest Service (Beets et al. 2003) with 63 relevés from 2002 and observed groundwater levels with starting dates ranging from 1974 to 1998 and end date 2002.

The relevés refer to vegetation types from different succession stages, on various soils (with sandy soils dominating), ranging from dry to very wet, from nutrient-poor to nutrient-rich and from acid to alkaline. Five phytosociological alliances are dominant in the datasets. Descriptions of these alliances are found in parts 2 and 3 of the vegetation description of The Netherlands (Schaminée et al. 1995, 1996). [2] and [3] added to the names in the following list refer to the respective references: *Nardo-Galion saxatilis*[3], *Calthion palustris*[3], *Ericion tetralicis*[2], *Caricion nigrae*[2] and *Caricion davallianae*[2]. Besides these types, that make up ca. 50% of the datasets, the relevés mainly belong to: *Lolio-Potentillion anserinae*[3] and *Junco Molinion*[3] (dataset A), *Empetrion nigri*[3] and *Hydrocotylo-Baldellion*[2] (B), *Empetrion nigri*[3] and *Oxycocco-Ericion*[2] (C).

Some terrestrial plant communities are characterized by groundwater levels close to, or even above, the soil surface in wet periods. None of the investigated plots had been under influence of a major change in hydrological conditions.

All vegetation relevés were recorded in The Netherlands, a small and flat country with a temperate climate that has small spatial differences in meteorological conditions. The spatial deviations in mean annual precipitation and reference evapotranspiration; the evapotranspiration of grassland under optimal water supply, according to Makkink (1957), are within 20% and 10% of the overall mean, respectively (Sluijter & Nellestijn 2002). The temporal variation in precipitation surplus (precipitation minus reference evapotranspiration) for The Netherlands is given in Fig. 1a, b.

The relevés of datasets A and B were distributed across the whole country and the relevés of dataset C were located mainly in the dune areas of the western and northern parts of The Netherlands. Because the spatial meteorological differences are small and because sandy soils dominate each dataset, systematic deviations in the relationships caused by the spatial prevalence of relevés within a dataset are not to be expected (see also the Discussion section).

The species composition of each dataset was recorded after periods with different meteorological conditions, as characterized by the precipitation surplus: dataset A follows a relatively average, B a dry and C a wet period, respectively (Fig. 1a). Differences in mean precipitation surplus were apparent over long periods of time: mean precipitation surplus of datasets A and B coincided when calculated over four years, but dataset C showed a consistently higher precipitation surplus for the whole time period of 30 years considered (Fig. 1b).

Extension and interpolation of groundwater level series

Fortnightly measurements of groundwater level data were available for each relevé, but only for a limited number of years. To analyze long time series of daily groundwater level data, the groundwater level series were extended to the period 1970-2000 and interpolated to daily values with *Menyanthes* (von Asmuth et al. 2002). The interpolation was needed to calculate *MSL* values accurately. *Menyanthes* is an impulse-response model, which transforms precipitation and evapotranspiration series (impulse) into groundwater level series (response). Local meteorological data on precipitation and reference evapotranspiration were available from the Royal Netherlands Meteorological Institute on a daily basis from 1970 onwards for stations with a maximum of 30 km (precipitation data) and 70 km (evapotranspiration data) from any relevé.

For each time series measured at a relevé, a *Menyanthes*-model was created that links the local

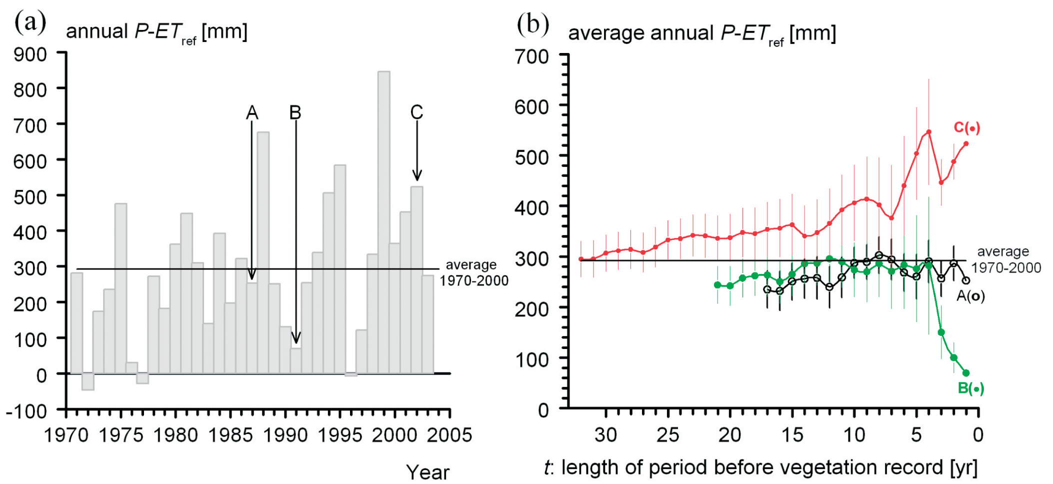

Fig. 1. Precipitation surplus data (difference between precipitation and reference evapotranspiration $P\text{-}ET_{ref}$) for De Bilt, the weather station in the centre of The Netherlands. (**a**) Annual $P\text{-}ET_{ref}$. Each bar represents the cumulative difference between precipitation and reference evapotranspiration for a hydrological year (e.g.: 2000 = 1 April 1999 - 31 March 2000). A, B, C: year of vegetation recording of the three datasets. (**b**) Average annual $P\text{-}ET_{ref}$, with standard errors, derived from (a), across t years preceding the vegetation recording, indicating deviations between datasets A, B and C and the long-term average. t = 1 year corresponds to the year of the vegetation recording for each dataset: 1987 for dataset A, 1991 for B and 2002 for C.

precipitation surplus series, as input to the hydrological system, to groundwater level series. Then, groundwater levels were simulated over the period 1970-2000 by feeding the fitted *Menyanthes*-models with the same local precipitation surplus series of daily values of the period 1970-2000.

Menyanthes presents the quality of a model in terms of the explained variance. We omitted relevés from the analysis with groundwater level series that could not be modelled in a reliable manner (explained variance < 70%; von Asmuth et al. 2006).

Calculation of MSL_t *and* F_m

At groundwater independent sites, vegetation composition has no causal relationship with groundwater level (Witte & von Asmuth 2003). Consequently, relevés coinciding with deep groundwater levels (*MSL* calculated from 1970-2000 data deeper than 1.3 m below soil surface) were omitted. Overall, 133, 45 and 54 relevés could be used for further analysis of dataset A, B and C, respectively.

For each relevé, harmonization of groundwater levels was achieved by computing MSL_t as the mean of the groundwater level at the first of April (van der Sluijs 1990) for *t* years preceding the vegetation recording:

$$MSL_t = \frac{1}{t} \sum_{t^*=1,t} gwl_{(1\text{April})t^*} \quad (1)$$

MSL_t was calculated for minimal t =1 year and maximal t =18 years (dataset A), 22 years (B) and 33 years (C). These maxima equal the period from 1970 to the year of the vegetation record (1987, 1991 and 2002, respectively). To avoid groundwater level fluctuation data biased by overly wet or dry years, three years is the minimum measuring period that should be considered (Mew et al. 1997; Wamelink et al. 2002). According to Knotters & van Walsum (1997), a period of at least t = 30 yr is needed to calculate a reliable mean groundwater level, representative of climatic conditions. Therefore, we also computed the *MSL* from simulated groundwater levels over the period 1970-2000. This *MSL* is referred to as MSL_{climate}.

A list of moisture indicator values for plant species tailored to The Netherlands based on expert judgment and national and international literature (e.g. Ellenberg 1992; Londo 1975), was used to compute the arithmetic mean moisture indicator value F_m for each relevé. Witte et al. (2007) compiled this list of indicator values from published ecological groups for vascular plants (Runhaar et al. 2004; Witte 2002), mosses and liverworts (Dirkse & Kruijsen 1993) and *Characeae* (van Raam & Maier 1993). The consistency of the division into ecological groups has been tested on a set of ca. 50 000 relevés from all over The Netherlands (Runhaar 1989). Indicator values were derived directly from the division of plant species into ecological groups, without the use of physical habitat factors such as groundwater level. All plant species present in each relevé were used to calculate

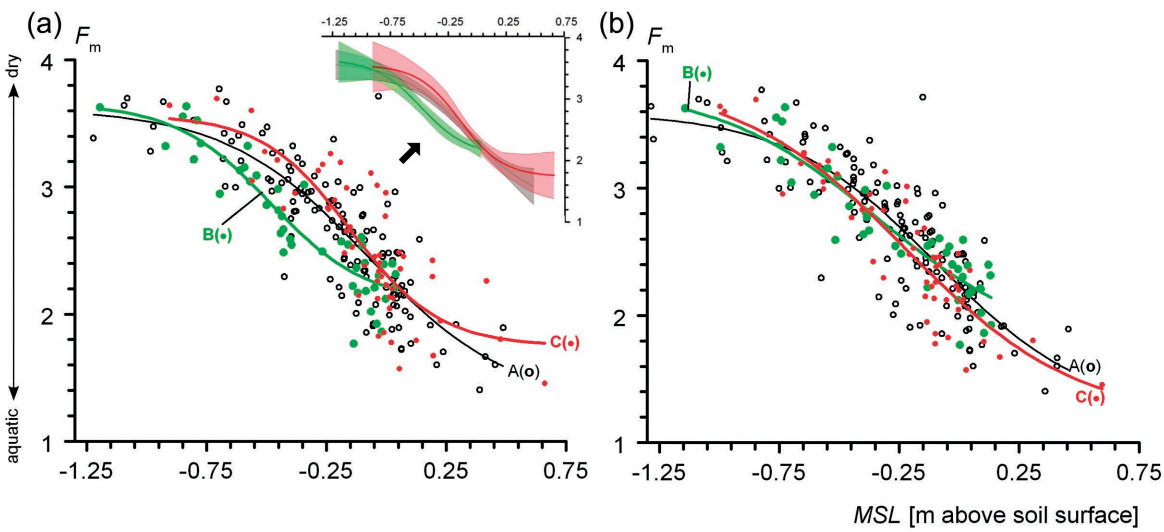

Fig. 2. Mean moisture indicator values of the vegetation (F_m) for datasets A, B and C, in relation to the mean spring groundwater level calculated (**a**) over three years (MSL_3) and (**b**) for average climatic conditions (1970-2000; MSL_{climate}). Each point represents a relevé. The insert in (a) shows the 95% confidence intervals for the relationships. Equations and correlation coefficients can be found in Table 3.

Table 1. Results of F-tests to compare sigmoid regression lines between MSL_t and F_m for t different periods. Significant differences ($p < 0.05$, corrected by False Discovery Rate; Benjamini & Hochberg 1995) are marked by *. Climate = 1970-2000.

Comparison of datasets:	A and B		A and C		B and C	
t (yr)	F	p	F	p	F	p
1	9.79	3.77E-07*	1.12	0.350	5.85	3.09E-04*
2	9.27	8.44E-07*	1.01	0.403	6.50	1.20E-04*
3	4.91	9.00E-04*	0.87	0.486	5.84	3.13E-04*
4	0.97	0.426	1.21	0.306	3.00	0.023
5	1.17	0.328	1.09	0.363	3.79	0.007*
6	1.12	0.348	1.25	0.290	3.97	0.005*
7	1.17	0.328	2.10	0.083	4.07	0.004*
8	1.12	0.347	1.73	0.146	4.45	0.002*
9	0.91	0.462	1.72	0.148	4.72	0.002*
10	0.78	0.541	2.07	0.087	4.63	0.002*
11	0.91	0.458	1.94	0.105	4.94	0.001*
12	1.09	0.363	1.90	0.113	5.00	0.001*
13	0.97	0.426	2.02	0.093	4.80	0.001*
14	1.00	0.410	1.81	0.129	4.83	0.001*
15	0.89	0.472	1.55	0.190	4.53	0.002*
16	0.88	0.475	1.43	0.226	4.33	0.003*
17	0.98	0.422	1.36	0.248	4.34	0.003*
18	0.84	0.501	1.40	0.235	4.25	0.003*
19	-	-	-	-	4.04	0.005*
20	-	-	-	-	3.85	0.006*
21	-	-	-	-	3.61	0.009*
22	-	-	-	-	3.66	0.008*
Climate	0.65	0.628	1.43	0.226	1.96	0.107

the vegetation characteristics of each relevé in terms of mean indicator values. Following the findings of Käfer & Witte (2004), no weight was given to species abundance. The indicator values range from one, for species from aquatic systems, to four, for species from extremely dry systems.

Statistical analysis

Theoretically, the relationship between MSL_t and F_m is confined by the two boundaries of the F_m-scale: $F_m = 1$ (aquatic) and $F_m = 4$ (dry). In practice, the range of F_m-values is smaller because of ecological reasons. Hence, the data points level off towards both ends of the indicator value scale (Witte & von Asmuth 2003). Relationships of this form can be described by sigmoid functions.

Sigmoid regression lines between MSL_t (independent) and mean indicator value for moisture (F_m) (dependent) were fitted to each dataset, using the least square method. Because of the asymptotes, sigmoids were physically more correct than linear regression lines for the considered ranges of MSLs. Furthermore, sigmoids were statistically better (the correlation coefficient r between predicted vs observed values is generally 0.02 higher). Residuals of the sigmoid relationships were normally distributed and not affected by the spatial configuration of the data.

Statistical differences between the shapes -in parts- of the empirical relationships based on dataset A, B and C were tested through an F-test (Motulsky & Christopoulos 2003).

To quantify the mean error in the prediction of F_m and the differences in the mean error when relationships are based on different periods t, cross-prediction was performed for MSL_3 and $MSL_{climate}$ data. For the cross-prediction, the relationships for t = 3 yr and t = climate from A, B and C were fed with MSL_3 and $MSL_{climate}$ values, respectively, of the other datasets and the root mean squared errors ($RMSE$s) of the predictions were calculated. The $RMSE$ represents the mean error that is made in F_m across the range of MSLs. Additionally, the Pearson correlation coefficients r between predicted and observed values of the cross-prediction were calculated.

Empirical relationships between MSL_t and F_m were also calculated for all datasets together (i.e. datasets A, B and C were merged) for an increasing number of contributing years t. The effect of t on the predictive value of this empirical relationship was tested by determining the significance of differences between Pearson's correlation coefficient r between predicted vs observed values for t = 1 to 18 yr (r_t) vs $r_{climate}$ using the method of Meng et al. (1992). This method compares two different correlation coefficients while taking account of dependencies between explanatory variables.

As multiple significance tests were executed on the same datasets, significant differences were corrected by False Discovery Rate (Benjamini & Hochberg 1995).

Results

The sigmoid relationship between F_m and MSL_3 was significantly different for dataset B compared to the other two datasets (Fig. 2a, Table 1). At F_m = 2-3, for instance, sigmoids B and C deviate 20-30 cm. The 95% confidence intervals show, that especially in this sloped part of the sigmoids, the sigmoids were statistically different.

The differences between the relationships coincided with differences in meteorological conditions during the measurement period. The dry years before the vegetation record of dataset B (Fig. 1a) resulted in relatively low MSL_3 values. Wetter conditions (as in dataset C) resulted in a shift of the sigmoid curve to the right, i.e. towards higher groundwater levels, although sigmoid C did not differ significantly from sigmoid A (Table 1).

Table 2. Results of cross-prediction indicating the change in predictive error (*RMSE*) and the change in correlation coefficient between predicted and observed values (r) of F_m based on *MSL*-values calculated over t = 3 yr and over t = climate. F_m-values were predicted with the regression parameters of one dataset and the *MSL*-values of another dataset. Climate = 1970-2000.

		RMSE			*r*	
MSL data	regression line	t = 3 years	t = climate	change %	t = 3 years	t = climate
A	B	0.36	0.30	18.2	0.79	0.84
B	A	0.29	0.21	26.3	0.89	0.91
A	C	0.30	0.30	-0.6	0.85	0.85
C	A	0.32	0.26	18.8	0.82	0.90
B	C	0.36	0.24	34.9	0.86	0.91
C	B	0.40	0.27	33.1	0.76	0.90

When considering a period of 4 years or more, the difference between sigmoids A and B became insignificant (Table 1). Again, this insignificant difference coincided with an insignificant difference in mean precipitation surplus from t = 4 years onwards (Fig. 1b). The very wet year of 1988 apparently compensated the dry period of 1989-1991. The differences in both precipitation surplus and sigmoid B and C remained significant for all t's observed (Table 1, Fig. 1b). Only in the case of MSL_{climate} did the three regression lines coincide and the (visibly small) differences became insignificant (Fig. 2b, Table 1).

The cross-prediction showed that only the *RMSE*s and the correlation coefficient r between predicted and observed values of cross-prediction of the *MSL*-data of dataset A on the regression lines of dataset C were not influenced by a different period t (Table 2). The decreases in *RMSE*s of the other cross-predictions of MSL_{climate} vs MSL_3 were 20 to 30%. This indicates that data harmonization (Table 1) substantially decreased prediction errors.

The increasing resemblance of the regression lines was associated with the number of years contributing to *MSL* and with differences in precipitation surplus in the sampling year compared to the mean precipitation surplus. For the same reason, there was an increasing resemblance of data points with increasing t in the combined datasets A, B and C, reflected by increased values for the Pearson's correlation coefficients r (Fig. 3). Conversely, r_1–r_3 were significantly different from r_{climate}. A peak in r occurred in the period that the meteorological conditions for datasets A and B were similar (Fig. 1b): r_4–r_8 were not significantly different ($p > 0.10$) from r_{climate}. For t = 9-18 year, r fluctuated around 0.856 (SD = 0.003). The small fluctuations in r and the low p-values (r_9–r_{16}: $p < 0.05$; r_{17}–r_{18}: $p < 0.10$) indicate that temporal deviations in meteorological conditions with respect to the climate conditions were still apparent in the defined relationship between *MSL* and F_m.

The relationships between *MSL* and F_m, based on harmonized data as well as the combined datasets, are described in Table 3.

Table 3. Values for coefficients that describe the sigmoid regression lines between MSL_t and F_m for t = 3 years and t = climate (1970-2000). ABC represents the combined datasets and ABC with t = climate represents the relationship between *MSL* and F_m based on harmonized data and the combined datasets.

Sigmoid regression lines are described by: $F_m = a + \frac{b}{\left(1+\exp\left(c+d\cdot MSL_t\right)\right)}$.

Last column: r correlation coefficient between predicted and observed values.

	t	*a*	*b*	*c*	*d*	*r*
A	3 years	1.29	2.32	0.26	3.39	0.85
	climate	1.21	2.39	0.29	3.17	0.85
B	3 years	2.09	1.57	2.41	5.00	0.91
	climate	1.73	2.06	1.01	2.96	0.91
C	3 years	1.75	1.82	0.81	5.43	0.90
	climate	1.18	2.67	0.62	2.84	0.83
ABC	3 years	1.41	2.23	0.44	3.25	0.84
	climate	1.19	2.51	0.36	2.84	0.87

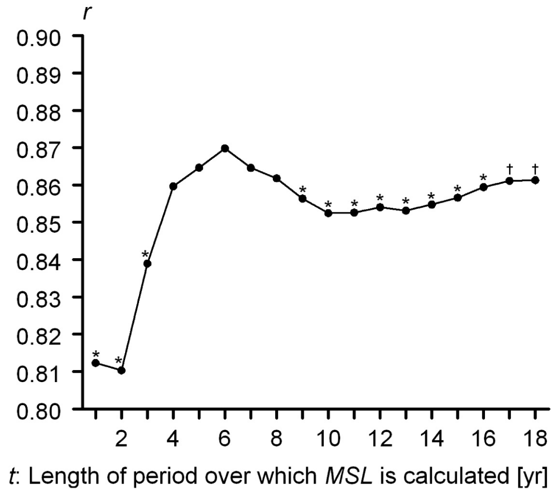

Fig. 3. Pearson's correlation coefficient r between observed and predicted values for relationships between MSL_t and F_m as a function of t. Significant differences (corrected by False Discovery Rate; Benjamini & Hochberg 1995) between r_t and $r_{climate}$ (0.87) are indicated by * ($p < 0.05$) and † ($p < 0.10$).

Discussion

Deriving relationships between environmental conditions and vegetation

Our analysis clearly shows that abiotic variables, including meteorological conditions, may need to be measured for long periods to remove systematic differences between empirical relationships and thus to derive general relationships between environmental conditions and vegetation characteristics. Some of the relationships found in literature are only valid for specific meteorological conditions, for instance after a number of very dry years and are thus not generally applicable.

We showed that basing relationships on short time series of abiotic measurements resulted in biased relationships and that harmonization of abiotic data in time removed the bias and led to relationships that are generally applicable. Furthermore, we showed that merging data from different sources without harmonization of data in time, resulted in large variation and thus low goodness of fit of the defined relationships. This fact was already brought to attention by Witte & von Asmuth (2003), but it was only hypothetical until now. This paper confirms the hypotheses of Witte & von Asmuth (2003) that: (1) fitting a model through data from different datasets will yield a poor fit and (2) that describing the moisture indicator value of the vegetation as a function of the climatologically averaged *MSL* produces a higher explained variance.

The relevés of dataset C were mainly confined to the dune area in the western and northern parts of The Netherlands. This confinement might have caused a systematically different relationship between *MSL* and F_m for datasets A and B. We checked if specific soil types (clay, loam, peat and sand) caused extra noise in the harmonized relationship. The *RMSE*s of relationships of each soil type were larger than the *RMSE* of all soil types together. This indicates that soil type did not cause systematic differences between the relationships. If soil type would have mattered, the three datasets would not have coincided when data were harmonized.

The harmonization of data in time includes two important aspects: (1) definition of an appropriate estimator of abiotic conditions and (2) quantification of historical relationships between vegetation and abiotic conditions, reflected by a certain present-day vegetation characteristic. Both aspects have to be, and implicitly were, considered simultaneously to come to unbiased relationships. In this paper, we used simple arithmetic means to harmonize groundwater levels. At the same time, we are aware that the abiotic conditions of 30 years ago will only have a minor contribution to the actual species composition. We therefore think that harmonization based on time-weighted means will increase the statistical significance of the relationships even more. Unfortunately, more process based functions weighing the abiotic history of sites are presently unavailable. Nevertheless, our results show that a limited period of abiotic measurements should be avoided, as there is a fair chance that it biases the derived relationships (Table 1). Even the maximum measurement period of 22 years for dataset B was still too short to make the regression line coincide with dataset C. Only a $MSL_{climate}$ based on 30 years of measurements was sufficient to create one uniform relationship. So, arithmetic means over long periods of time (up to 30 years) improved the robustness of the relationships. Presumably, if weighted means would have been used, the abiotic conditions of 30 years ago would still have had a significant weight. This indicates that the mean vegetation composition of the relevés from each of the three datasets reflect the relationships between vegetation and abiotic conditions over a long period in the past and thus that generally the relevés have a large delayed response. If one of the three datasets would have been dominated by relevés with a small delayed response, the regression lines would never have coincided when considering the same period preceding the vegetation recordings for each comparison. We hypothesize that incorporation of formulations on the delayed response of functional species groups (like annual and perennial species), as a further refinement of deriving relationships between environmental conditions and vegetation, might result in an even higher predictive value of relationships.

Extrapolation to other relations between vegetation and abiotic conditions

As well as the relationship between soil moisture regime, described by *MSL*, and vegetation characteristics, the problem outlined here also applies to relationships of vegetation characteristics to other soil parameters such as soil nitrogen content, soil phosphate content and soil pH or climatic variables such as temperature, that vary stochastically in time (Cain et al. 1999; Farley & Fitter 1999; Kieft et al. 1998). For three reasons, the time period to be considered for these relationships will be different from the one identified here. Firstly because each abiotic process has its own specific characteristic time constant, which quantifies the long-term fluctuations of the entity (e.g. pH or concentration of soil chemical parameters). This characteristic time will vary from weeks to centuries, depending on the time scale of the dominant process (e.g. adsorption, erosion or precipitation surplus, as in this study). Secondly, the characteristic time of the vegetation is important. In this paper we used mean indicator value, a constant, which by definition has a large characteristic time as indicator values are representative for equilibrium conditions. Other vegetation characteristics, e.g. the formation of aerenchyma (also related to soil moisture conditions) or specific leaf area may have shorter time constants, since these also vary within species. Thirdly, the considered time period depends on the relationships between plant species and abiotic parameters. Particularly disturbances causing e.g. nutrient pulses through vegetation die-back (e.g. van Bodegom et al. 2006) and feedbacks, e.g. those controlling nutrient losses (e.g. Knops et al. 2002), are important in this respect.

All these factors are known qualitatively, but quantitative knowledge is lacking. This implies that the optimal period over which data have to be harmonized should be determined empirically. The data harmonization procedure, outlined and exemplified in this paper, can be used for this in combination with existing process-based models on the abiotic conditions of consideration like nitrogen dynamics (e.g. Rastetter et al. 1997), available phosphorus (e.g. Grant & Heaney 1997) or acidity (e.g. Wade et al. 1999). Through these models, error propagation, inherent to interpolation and extrapolation involved in data harmonization procedures, can be minimized. With time series of abiotic conditions thus derived, an analysis similar as to ours can be used to obtain generally applicable relationships.

Conclusion

Single and short term field measurements of abiotic conditions are likely to deviate from the mean conditions reflected by vegetation characteristics. Without data harmonization, relationships among these variables are only valid for environmental conditions resembling those during the collection of field data. Application to other conditions leads to systematic prediction errors and is dissuaded. This problem can be overcome by harmonization of abiotic data in time as this (1) eliminates biased measurements, (2) results in general applicable relationships between abiotic and vegetation characteristics and (3) increases the goodness of fit of these relationships. The presented harmonization procedure can be used to optimize many relationships between abiotic conditions and vegetation characteristics by generating time series through process-based models.

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