Acta Bot. Neerl. 47(3), September 1998, p. 337–349

Behaviour of wetland plant species along a moisture gradient in two geographically distant areas

W. KOTOWSKI*†, R. VAN DIGGELEN* and J. KLEINKE‡§

**Laboratory of Plant Ecology, Centre for Ecological and Environmental Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands; and ‡Botanisches Institut, Ernst Moritz Arndt Universität, Grimmer Straße 88, 17487 Greifswald, Germany*

SUMMARY

The occurrence of a species along an environmental gradient can be considered as the product of its physiological requirements and competitive interactions with other species. One may, therefore, expect that this *realized habitat* differs between areas when a species has to co-exist with different species. To test this hypothesis, we compared the responses of wetland plants to hydrological conditions in two European lowland river valleys: the Drentse A valley (The Netherlands) and the Peene valley (eastern Germany). We used *mean water level* and *water level amplitude* as hydrological parameters to analyse differentiation in realized habitats within species. Most species occurred in slightly wetter conditions, with higher fluctuations in the German site but with narrower tolerances for these parameters. We suggest that this may result from a higher competition intensity for light, possibly caused by a larger local species pool and/or presence of more dominant species with a high competitive ability. The consequences for practical applications—such as parameter estimation for predictive models—are discussed.

Key-words: competition, groundwater level, habitat, wetlands.

INTRODUCTION

The tolerances of species to ecological factors may differ when a species grows in a monoculture or in a mixture with other species (Ellenberg 1952, 1954; Austin & Austin 1980; Austin 1982; Aarsen & Epp 1990; Keddy *et al.* 1994). This phenomenon has been given a theoretical basis in association with terms such as *fundamental* vs. *realized* niche (Hutchinson 1957; Miller 1967) or *physiological* vs. *ecological* response (Mueller-Dombois & Ellenberg 1974). Differences between the two pairwise contrasts were generally supposed to be due to competition, but Ernst (1978) emphasized that several other factors could also affect species' occurrences. When data of species' distribution along environmental gradients are obtained from field studies it is difficult to judge

---

† Present address: Department of Sustainable Agricultural Land Development, Institute for Land Reclamation and Grassland Farming at Falenty, 05-090 Raszyn, Poland; Fax: +48 22 628 37 63, e-mail: W.Kotowski @biol.rug.nl.

§ Present address: Otto Grotewohlring 4, Bergen (Rügen), Germany.

whether they describe actual requirements or a set of co-influencing factors. Hence, the term *habitat* seems less ambiguous than the term *niche* when describing the set of conditions where species occur (Looijen 1995).

Actual measurements of *realized habitats* consist normally of an analysis of the occurrence of plant species along environmental gradients, often with the aim of developing predictive models of vegetation changes in a changing environment (Van Diggelen *et al.* 1991b; Austin 1992; Keddy 1992; De Swart *et al.* 1994; Noest 1994; see Grootjans & Van Diggelen 1995). A limitation of all predictions is the assumption that the correlation found will remain constant under new conditions. Influences of different biotic conditions, i.e. interactions with species not present in the studied communities, are usually neglected as well as the fact that local ecotypes of species may differ in their physiological requirements and thus in realized niches and habitats (e.g. Kik *et al.* 1991; Knapp & Rice 1996). Several authors have therefore concluded that one should be very careful when extrapolating species response curves to regions other than where the data were collected (Niemann 1973; Grootjans *et al.* 1993; Wierda *et al.* 1997). Similarly, an extrapolation over a long time period also seems potentially dangerous because of unpredictable interactions with new competing species (Westman 1991).

However, the amount of variation in the realized habitats of species in natural communities is not clear. Warnings about data extrapolation are based mainly on experimental studies while comparative field studies of species behaviour in different geographical regions are lacking. Therefore, answers are not yet available to the following questions: to what extent can we use autecological data from one area to predict species behaviour in another area? Are there species which are more constant in their occurrence along environmental gradients and hence are more universal indicators and, if so, which species are they?

In this paper, we explore these questions for fens and wet meadows. In these ecosystems the groundwater regime is considered to be a major factor which affects water availability directly and nutrient supply indirectly, namely by controlling the peat mineralization rate (Grootjans *et al.* 1985, 1986; Kemmers 1986; Van Diggelen *et al.* 1991a, 1991b; Wierda *et al.* 1997). The relationship between species occurrence and water level is therefore a very important factor in predictive models for wetlands. The need to verify these relationships 'in different types of landscape, with different geology and climate' was stressed by Grootjans *et al.* (1993). In response to this demand we compare the responses of wetland species to hydrological factors in two geographically distinct areas with similar riparian vegetation: the Drentse A valley in The Netherlands and the Peene valley in eastern Germany. The study areas are separated by a distance of about 600 km. The comparison is based on the analysis of two existing databases.

Species response models

Methods for the analysis of species–environment relations are developing quickly (e.g. Austin 1987, 1992; Ter Braak & Gremmen 1987; Keddy 1992; Huisman *et al.* 1993; Wierda *et al.* 1997) and currently response regression models are most commonly used for this purpose. This method is believed to give more accurate results than the previously used weighted averaging technique, which disregards the absence of species and is more influenced by sampling pattern (Ter Braak & Gremmen 1987). Ter Braak and Looman (1986) showed, however, that regression analysis is mainly advantageous in the case of large datasets with many positive values for species' occurrence or when the distribution of samples along the environmental gradient is very uneven (see also Ter Braak & Barendregt 1986; Jongman *et al.* 1987). Otherwise, the simpler method of weighted averaging seems sufficient. In the case of the hierarchical set of response models presented by Huisman *et al.* (1993), which provides more information about the response of species (particularly skewness of the curve), there is no consistent measure of tolerance (Huisman *et al.* 1993); hence no standard statistics can be applied to compare the calculated indicator values. Since the comparison of species' occurrence patterns in two areas is the main objective of this study, we chose the method of weighted averaging.

STUDY AREAS

The Peene valley

The sites lie in the valley of the River Peene in north-eastern Germany between the city of Anklam (53 50′N, 13 42′E) and lake Kummerower See (53 47′N, 12 53′E). The valley lies in the end-moraine landscape of the Baltic glaciation and is filled with peat deposits of over 10 m deep. The availability of marl in the subsoil beneath the peat enables enrichment of calcium in the groundwater (Kleinke 1968).

The area has an oceanic climate with mild winters (average January temperature of −1·0°C) and rather cool summers (average July temperature of 18·1°C). The annual precipitation is about 600 mm.

The landscape of the Peene valley is relatively undisturbed and consists of relics of species-rich meadows and fens. Especially at the time of data collection (the 1960s), the landscape was relatively slightly affected by man; it was fertilized at a low level and mainly used for hay-making.

The Drentse A valley

These sites lie in the stream valley nature reserve 'Drentse Aa' in the northern part of The Netherlands (53 03′N, 6 39′E). The river drains a ground moraine plateau of *c.* 200 km^2 on top of Pleistocene nutrient-poor sands. Geological investigations show thick layers of relatively mineral-rich meltwater sands underneath (WRGOD 1978). The valley itself is filled with peat layers of *c.* 4 m thickness. The groundwater is base-rich—the calcium content in particular can be substantial. This is leached away from deeper sandy layers which are not decalcified. Large concentrations of Fe^{2+} ions have also been noticed in some places. More detailed hydrological descriptions of this region are presented by Grootjans (1985) and Everts and De Vries (1991).

This area also has an oceanic climate (average January temperature 0·9°C, July 16·7°C). The annual precipitation here is, on average, 812 mm.

In comparison to the Peene valley, the Drentse A valley has experienced a higher degree of anthropogenic pressure. Most of the area was moderately drained and the agricultural use continued to intensify until the 1960s, leading to the fragmentation of characteristic plant communities (Everts & De Vries 1991). From 1966 onwards the nature conservation organization *Staatsbosbeheer* bought lands in this area and started restoration management, aimed at the recovery of former botanical values. This management consisted of blocking the drainage ditches and instituting a mowing regime

Table 1. Pearson correlation coefficients within the major parameters characterizing the hydrological regime

	Amplitude	Mean	Mean highest	Mean lowest
Amplitude	1	−0·32***	0·126 NS	−0·543***
Mean		1	0·842***	0·921***
Mean highest			1	0·764***
Mean lowest				1

****P*<0·001; NS, non-significant. For explanation of terms see text.

without fertilization; so the sites in the Drentse A area are partly relics of former species-rich meadows and partly regenerating sites.

METHODS

Data

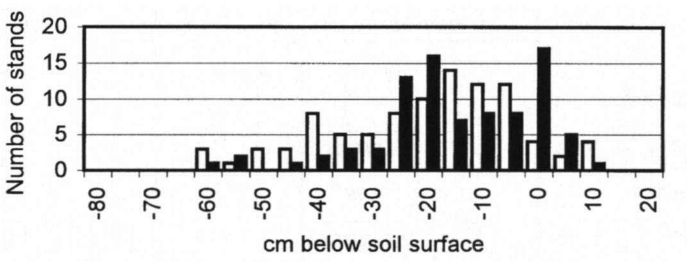
The data for this study comprise those sampled by Kleinke (1968) in the Peene valley between 1965 and 1967 and by the Laboratory of Plant Ecology, University of Groningen in the Drentse A valley in the period 1966–81 (unpublished data). All data consisted of vegetation relevés together with regular measurements of the groundwater level at the recorded sites. A total of 94 records from the Drentse A valley and 86 records from the Peene valley were analysed. Vegetation types investigated represent riparian meadows and wetlands in different forms along a wetness gradient. In particular, plant communities from the alliances *Calthion palustris*, *Molinion caeruleae*, *Caricion curto-nigrae* and *Magnocaricion* are included. The relevés were recorded from homogeneous vegetation stands using plots ranging from 2 × 2 m to 4 × 4 m.

The groundwater level was measured in a piezometer at each point at least once a month but normally every 2 weeks during the vegetative period (15 March–20 October) over at least 2 years at each site. We used only data from sites where there was no significant interference with the hydrology for at least 10 years.

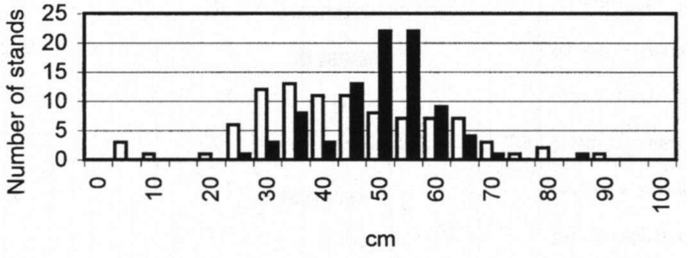
To avoid truncation of species distributions, we analysed a wetness gradient which was as long as possible without changes in other relevant habitat parameters: the soil type was restricted to peat only, and possible effects of differences in pH were minimized by using only groundwater-fed sites. We chose samples in such a way that each plant association was represented by approximately the same number of samples to avoid effects of sampling size on the calculated responses of species.

Hydrological parameters

The measurements of water level were used to calculate daily water level depths by linear interpolation from which four hydrological parameters were calculated: mean lowest water level (low), mean water level (mean), mean highest water level (high) and water level amplitude (amplitude). Low and high were calculated from a moving average of the water level, calculated over 31-day periods. The lowest average is the mean lowest level (low), the highest average is the mean highest level (high). Amplitude is calculated as the difference between these two values. Further analysis showed that three factors characterizing the wetness of a site (low, mean, high) were strongly correlated with each other and not or only slightly correlated with amplitude (Table I)



Mean water level



Water level amplitude

Fig. 1. Distribution of the hydrological parameters in the two datasets. Two-tailed significance of comparison: for mean, Levene's test, $P=0{\cdot}071$, t-test, $P=0{\cdot}117$; for amplitude, Levene's test, $P<0{\cdot}001$, t-test, $P=0{\cdot}033$. □, Drentse A; ■, Peene.

which is consistent with the results of Wierda *et al.* (1997). We reduced the number of parameters to two but unlike Wierda *et al.* (1997), who proposed high and amplitude, we used mean and amplitude to make a comparison with other studies possible (e.g. Grootjans & ten Klooster 1980; Wheeler & Shaw 1987; Scholle & Schrautzer 1993). The means of those two parameters were compared statistically between the two datasets using Student's t-test for equality of means, while the variances were compared using Levene's test for homogeneity of variances.

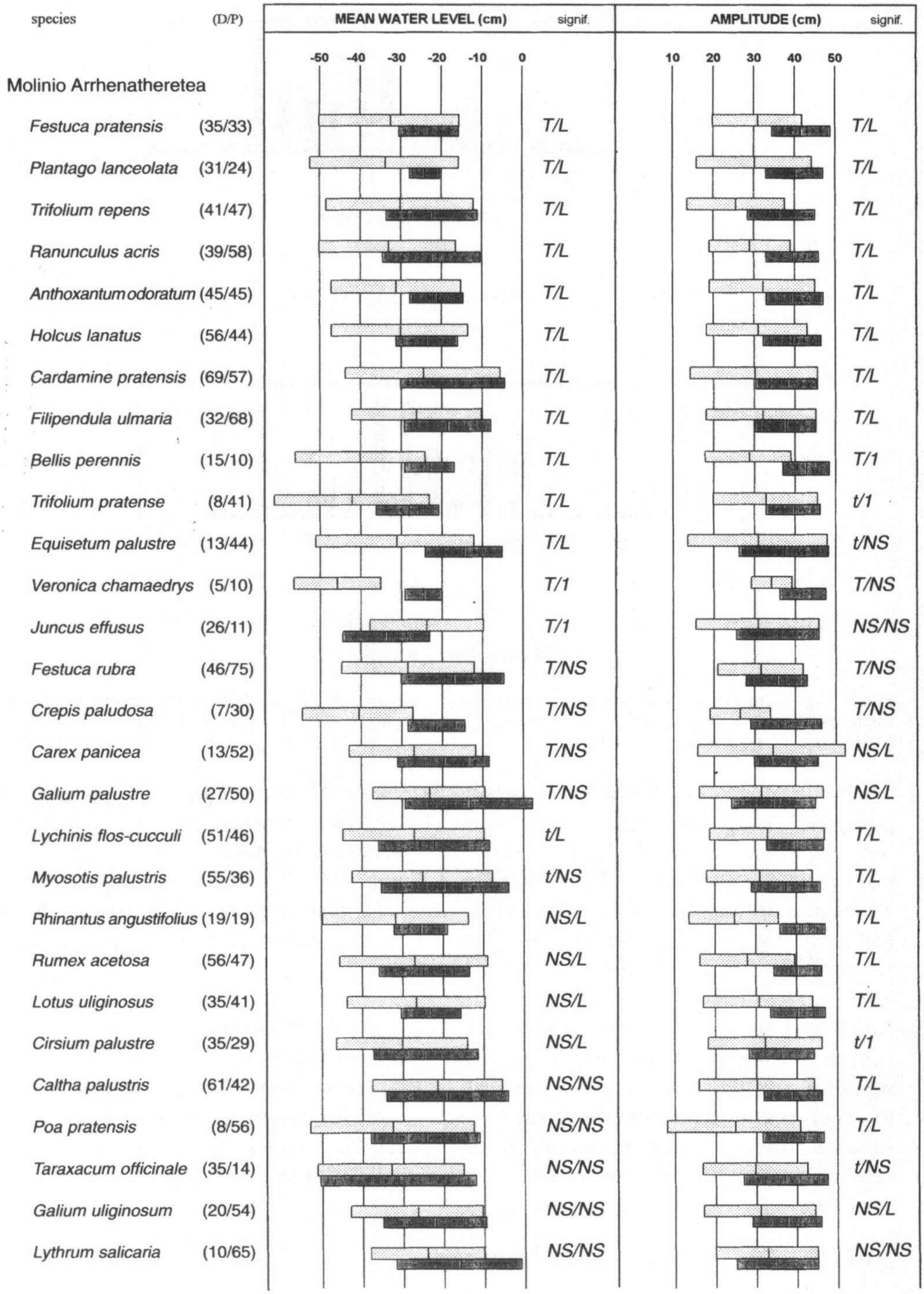
Calculation of indicator values and comparison between the areas

Indicator values for mean water level and water level amplitude were calculated by weighted averaging for presence–absence data under the constraint that a species had to occur in at least five relevés in each area. A t-test for independent samples was used for each species to compare the calculated averages between the two areas and Levene's test to compare the variances. The significance level of the comparison is given for each species.

RESULTS

Comparison of sampling patterns

Figure 1 presents the distribution of the two parameters in the sampling patterns for the two areas. The two datasets do not differ significantly according to mean water


species
(D/P)
MEAN WATER LEVEL (cm)
signif.
AMPLITUDE (cm)
signif.
-50 -40 -30 -20 -10 0
10 20 30 40 50
Molinio Arrhenatheretea
Festuca pratensis (35/33) T/L T/L
Plantago lanceolata (31/24) T/L T/L
Trifolium repens (41/47) T/L T/L
Ranunculus acris (39/58) T/L T/L
Anthoxantum odoratum (45/45) T/L T/L
Holcus lanatus (56/44) T/L T/L
Cardamine pratensis (69/57) T/L T/L
Filipendula ulmaria (32/68) T/L T/L
Bellis perennis (15/10) T/L T/1
Trifolium pratense (8/41) T/L t/1
Equisetum palustre (13/44) T/L t/NS
Veronica chamaedrys (5/10) T/1 T/NS
Juncus effusus (26/11) T/1 NS/NS
Festuca rubra (46/75) T/NS T/NS
Crepis paludosa (7/30) T/NS T/NS
Carex panicea (13/52) T/NS NS/L
Galium palustre (27/50) T/NS NS/L
Lychinis flos-cucculi (51/46) t/L T/L
Myosotis palustris (55/36) t/NS T/L
Rhinantus angustifolius (19/19) NS/L T/L
Rumex acetosa (56/47) NS/L T/L
Lotus uliginosus (35/41) NS/L T/L
Cirsium palustre (35/29) NS/L t/1
Caltha palustris (61/42) NS/NS T/L
Poa pratensis (8/56) NS/NS T/L
Taraxacum officinale (35/14) NS/NS t/NS
Galium uliginosum (20/54) NS/NS NS/L
Lythrum salicaria (10/65) NS/NS NS/NS

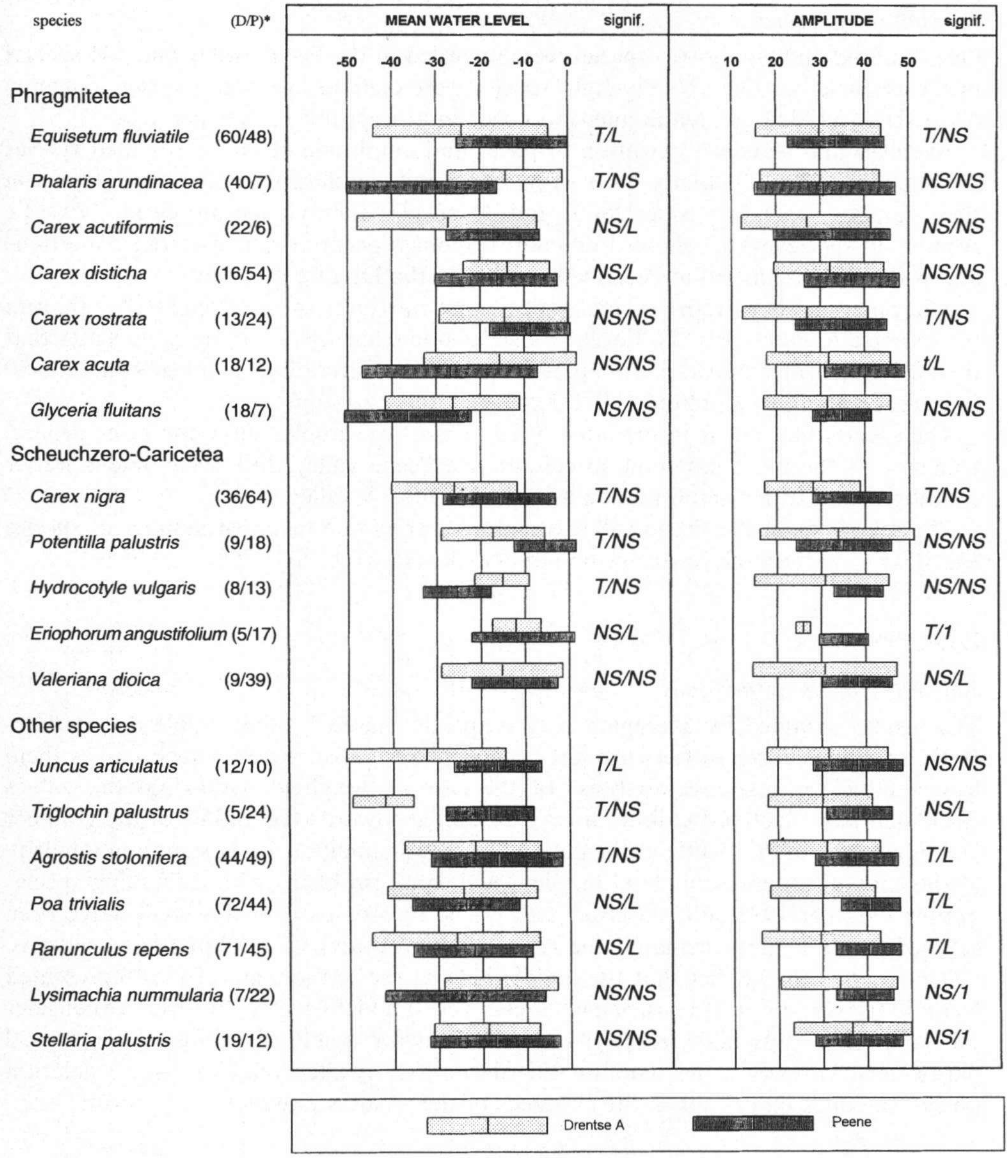


Fig. 2. Comparison of ecological responses of individual species to two hydrological parameters; bars reflect standard deviation from average; the average is indicated as black stripe at each bar. (D/P), number of species' records from which the average is calculated in the Drentse A valley (D) and in the Peene valley (P). Signif., statistical significance of: Student's *t*-test/Levene's test: *T*, *L*=$P<0.05$; *t*, *l*=$0.05<P<0.1$; NS=$P>0.1$.

level, but they do differ in water level amplitude. This implies that the results regarding amplitude may be influenced partly by differences in sample distribution and should be regarded with caution.

Responses of species

One hundred and eighty-two species were recorded in the Peene valley and 144 species in the Drentse A valley. Ninety-eight species were common to both datasets but only 47 of them fulfilled our requirement to occur in at least five relevés per area.

Averages and standard deviation of mean and amplitude of all investigated species are shown in Fig. 2. Twenty-seven species differed significantly between the areas in their response to mean water level, and 31 species for average amplitude ($P<0{\cdot}1$). Almost all species which showed different responses occurred under wetter conditions and wider amplitude in the Peene valley than in the Drentse A valley.

The ranges of occurrence of most species are narrower in the Peene valley than in the Drentse A valley (Fig. 2). Levene's test for homogeneity of variances indicates that the variances differ between the areas for 25 species according to mean, and for 30 species according to amplitude ($P<0{\cdot}1$).

The species that occur in one area in less than five samples show the same general tendency as the more common species. In the Peene valley they occur under wetter conditions and wider amplitude than in the Drentse A valley.

The relevés from the Peene valley are more species-rich (average number of species 34, SD = 13·4) than relevés from the Drentse A valley (20, SD = 8·0).

DISCUSSION

Reliability of the estimations

The results obtained by averaging may be partly biased by the sample distribution. Both hydrological parameters are not homogeneously distributed, which makes them less suitable for response analysis. In the case of weighted averaging, the values calculated from such a distribution may be shifted towards the middle of the gradient (Jongman *et al.* 1987) while in the case of regression analysis a low sampling intensity at the ends of an environmental gradient will cause problems with estimating species optima (Mohler 1983; Wierda *et al.* 1997). The records used in this study have been selected by taking approximately the same number of samples in all plant associations, which resulted in the fact that the middle part of the wetness gradient is represented by more relevés, simply because it has a higher vegetation diversity. However, we consider this solution as less undesirable than a selection for evenly distributed hydrological parameters. This would mean dominating the dataset by a few relatively rare vegetation types—the ones that occur at the extremes of the wetness gradient.

Consistency of realized habitats in wetlands

The results of the present comparison show that the ecological responses of the majority of the species to hydrological parameters are rather similar in both areas but there are also certain differences. The realized habitats of most wetland species are generally narrower in the German site than in the Dutch site and usually shifted towards wetter conditions and higher water level fluctuations.

The two areas have in common the fact that most species were more consistent in their responses to the mean water level than to the water level amplitude. This suggests that the general wetness of a site is ecologically more relevant than the fluctuation pattern. This should not be surprising. In contrast to the situation in severely degraded organic soils (Boelter 1974; Okruszko 1995) the capillary rise and water retention capacity of undrained or only slightly drained peats is sufficient to compensate the effects of water table fluctuations of a least 50 cm for a longer period and temporarily even more (Van der Sluys 1990). Problems with the availability of sufficient water are, therefore, unlikely in both areas. A much more plausible explanation lies in the influence of soil moisture content on nutrient availability (Grootjans *et al.* 1985, 1986; Koerselman & Verhoeven 1995; Okruszko 1995).

The source of differences in species' behaviour between two localities could be either genotypic variation in species' physiological tolerance or differences in biotic and/or abiotic conditions in the two regions. The first explanation, although possibly relevant, has to remain unsolved, for we have no means to explore it. We will, therefore, restrict ourselves to characteristics of the two regions when searching for what might have caused differences in species' behaviour.

The present study was undertaken with the assumption that the differences in abiotic conditions between the two areas are negligible, but this might not be entirely true. The climates of the two regions are both classified as 'oceanic', but the German site is slightly more 'continental' than the Dutch site. However, this explanation implies that the (physiological) tolerance of certain species is exceeded in one of the sites. This may be the case for a few species but, given the commonness of many species, we can hardly believe this to true in general.

A second explanation could lay in different histories of land-use in the two regions (see description of study areas) and their possible effect on soil properties. The two valleys are both filled with deep peat soils and both fed by groundwater of similar chemical composition but in the past agricultural pressure was somewhat higher in the Drentse A valley. Although still very modest, the drainage intensity was higher than in the Peene valley and this could have differently affected peat mineralization and decomposition. It may have increased nutrient availability somewhat while capillary rise may have decreased slightly, and both could have influenced the relationship between groundwater level and performance of plant species.

However, what differentiates the two regions much more clearly than habitat conditions is the composition of plant communities. Almost half of all the species from the Peene valley and one-third of the Drentse A valley are present in only one of the datasets. The total number of species and the mean number of species per relevé were, respectively, 1·26 and 1·7 times higher in the Peene dataset than that from the Drentse A. Given these large differences in species-richness in the two areas biotic interactions are expected to be different and interspecific competition could affect the size of realized habitats of individual species. The narrower ecological responses of species in the Peene valley could result from higher competitive pressure (Keddy *et al.* 1994) here than in the Drentse A valley due to a larger local species pool (cf. Zobel 1997) in north-eastern Germany than in the northern Netherlands and/or of differences in growth forms of the species that are unique for each area. Both explanations are likely to be true. The higher species richness in the Peene valley is discussed above but the growth forms and, therefore, competitive ability (see Keddy *et al.* 1994) of the species unique to one area also seem different. Analysis of the relevés shows that more species specific for the Peene valley are dominants (according to their cover in the relevés) than is the case in the Drentse A valley. Such dominants typical of the German study site are: *Geum rivale*, *Polygonum bistorta*, *Angelica sylvestris*, *Calamagrostis stricta*, *Cirsium oleraceum*; among the species restricted to the Dutch study site only *Carex aquatilis* occurs in high abundance. The above-listed species, characteristic of the Peene valley, are all relatively tall plants with large shade-casting leaves—they possess the traits of good light competitors (Keddy *et al.* 1994), while in the Drentse A valley such plants are lacking—most dominants are monocots. This may imply that light suppression by the canopy is lower here than in the Peene valley and hence the effect of competition on the realized niches (and the realized habitats) of plants might also be less.

That realized niches of plants become narrower due to competitive pressure of other species was reported from experimental studies of Austin and colleagues (Austin & Austin 1980; Austin 1982). However, shifts in the ecological optima along the nutrient gradient in comparison to those measured in a monoculture occurred only for a few species. The early competition experiments of Ellenberg (1952, 1954) also show that the competitive effect of neighbouring species is larger in the peripheral parts of the species physiological spectrum than near the physiological optimum. This would explain why the differences found in the present study are mainly in the width of the realized habitats and less in their location along the moisture gradient.

In our opinion, all explanations presented above are probably correct to a certain extent. The differences of competitive pressure due to different dominant species and species pools in the two regions are likely to affect the width of realized habitats of species; climatic conditions could explain a shift towards wetter sites in the Peene valley. However, the most spectacular difference in realized habitats is a total absence of a species from one area. As a consequence, the light conditions are better here and more 'space' can be occupied by other species. This effect of competition is probably accompanied by the results of the different histories of the areas. The Peene valley of the 1960s was a well preserved remnant of a former riparian landscape and maintained presumably a less disturbed vegetation zonation than the Drentse A valley, which has experienced more anthropogenic pressure in the past. So it is very likely that the relationships between hydrological regime and vegetation composition are less well established in the latter area. The fact that many characteristic fen species are rare or completely absent here could also suggest that the Drentse A valley is a regenerating, not-yet-stable system.

Relevance to conservation and restoration ecology

The problem of consistency of realized habitats remains very relevant when the data on the ecological responses of species are being extrapolated through time or space. Judgements of restoration scenarios depend regularly on information from reference sites which are sometimes located far from the area of restoration. In wetlands, processes controlling development of particular vegetation types seem to be similar even in quite distant regions (e.g. Wassen *et al.* 1996) but it is unclear how consistent species are in their response to (changes in) abiotic factors.

The results of the present study give some insight into this issue but do not provide a clear answer. The differences of species behaviour in the two areas are often surprisingly small, but the fact that many species can realize much narrower habitat in one area should warn us against extrapolating species–environment models outside the studied area. In our case, it can be concluded that reliable estimations for many species can be made by extrapolating data from eastern Germany to the Netherlands where the realized habitats are broader. Care should be taken, however, with predictions in the opposite direction, especially when estimating the tolerances of species. In restoration ecology it is usually more dangerous to overestimate than to underestimate them. If we assume that differences in the relationships between species performance and hydrological characteristics of sites are due partly to different intensities of anthropogenic pressure, the conclusion should be that extrapolations are possible from the lesser modified landscapes only. As there are currently very few areas, which are not significantly influenced by human activities, the task of data extrapolation is becoming more and more hazardous. Furthermore, as ecologists have to look for the unattached reference areas increasingly distant from the area of restoration, the chance of different biotic and abiotic backgrounds of niche or habitat differentiation in those regions is also becoming higher.

We conclude that, although good predictions of the realized habitats of many species can be achieved by extrapolating data from reference areas, it is always necessary to check these relationships at the local level. If available, local datasets are probably superior to data from more distant areas, even if the latter sets are larger. Extrapolations based on datasets which are too far apart should be avoided, especially when the flora of the target community differs much from the flora of the area where the data were collected.

ACKNOWLEDGEMENTS

This work was supported by a grant from the Dutch Organization for Scientific Research NWO (grant 805-35·853). Jacqueline Van Nugteren collected most of the Dutch field data, Latzi Fresco assisted with the numerical processing and Sue Shaw improved our English. Ab Grootjans, Jelte Van Andel and Eddy Van der Maarel, and two anonymous referees, commented on earlier versions of this paper and made suggestions for improving the text. We thank them all for their help.

REFERENCES

Aarsen, L.W. & Epp, G.A. (1990): Neighbour manipulations in natural vegetation: a review. *J. Veg. Sci.* **1:** 13–30.

Austin, M.P. (1982): Use of a relative physiological performance value in the prediction of performance in multispecies mixtures from monoculture performance. *J. Ecol.* **70:** 559–570.

Austin, M. P. (1987): Models for the analysis of species' response to environmental gradients. *Vegetatio* **69:** 35–45.

Austin, M.P. (1992): Modelling the environmental niche of plants: implications for plant community response to elevated CO2 levels. *Aust. J. Bot.* **40:** 615–630.

Austin, M.P. & Austin, B.O. (1980): Behaviour of experimental plant communities along a nutrient gradient. *J. Ecol.* **68:** 891–918.

Boelter, D.H. (1974): The hydrologic characteristic of undrained organic soils in the Lake States. In: Aandal, A.R., Buol, S.W., Hill, D.E. & Bailey, H.H. (eds): *Histosols, Their Characteristics, Classification, and Use.* SSSA Special Publication Series no. 6, Madison.

De Swart, E.O.A.M., Van der Valk, A.G., Koehler, K.J. & Barendregt, A. (1994): Experimental evaluation of realized niche models for predicting responses of plant species to a change in environmental conditions. *J. Veg. Sci.* **5:** 541–552.

Ellenberg, H. (1952): Physiologisches und ökologisches Verhalten derselben Pflanzenarten. *Berichte der Deutschen Botanischen Gesellschaft* **65:** 351-362.

Ellenberg, H. (1954): Über einige Fortschritte der Kausalen Vegetationskunde. *Vegetatio* **5–6:** 199–211.

Ernst, W. (1978): Discrepancy between ecological and physiological optima of plant species. A reinterpretation. *Oecol. Plant.* **13:** 175–188.

Everts, F.H. & De Vries, N.P.J. (1991): De vegetatieontwikkeling van beekdalsystemen. Een landschapsoecologische studie van enkele Drentse beekdalen. Historische Uitgeverij Groningen.

Grootjans, A.P. (1985): *Changes of groundwater regime in wet meadows.* Doctoral Thesis. University of Groningen, Groningen, The Netherlands.

Grootjans, A.P., Schipper, P.C. & Van der Windt, H.J. (1985): Influence of drainage on N-mineralization and vegetation response in wet meadows. I:

Calthion palustris stands. *Oecol. Plant.* **6**: 403–417.

Grootjans, A.P., Schipper, P.C. & Van der Windt, H.J. (1986): Influence of drainage on N-mineralization and vegetation response in wet meadows. II: *Cirsio-Molinietum* stands. *Oecol. Plant.* **7**: 3–14.

Grootjans, A.P. & ten Klooster, W.P. (1980): Changes of groundwater regime in wet meadows. *Acta Bot. Neerl.* **29**: 541–554.

Grootjans, A.P. & Van Diggelen, R. (1995): Assessing the restoration prospects of degraded fens. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J & Robertson, R.A. (eds): *Restoration of Temperate Wetlands*, pp. 73–89. Wiley, Chichester.

Grootjans, A.P., Van Diggelen, R., Everts, H.H., Schipper, P.C., Streefkerk, J., De Vries, N.P.J. & Wierda, A. (1993): Linking ecological patterns to hydrological conditions on various spatial scales: a case study of small stream valleys. In: Vos, C.C. & Opdam, P. (eds): *Landscape Ecology of a Stressed Environment*, pp. 60–75. Chapman & Hall, London.

Huisman, J., Olff, H. & Fresco, L.F.M. (1993): A hierarchical set of models for species response analysis. *J. Veg. Sci.* **4**: 37–46.

Hutchinson, G.E. (1957): Concluding remarks. *Cold Spring Harbour Symposia on Quantitative Biology* **22**: 415–427.

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, O.F.R. (eds) (1987): *Data Analysis in Community and Landscape Ecology.* Pudoc, Wageningen.

Keddy, P.A. (1992): Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3**: 157–164.

Keddy, P.A., Twolan-Strutt, L. & Wisheu, I.C. (1994): Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? *J. Ecol.* **82**: 635–643.

Kemmers, R.H. (1986): Perspectives in modelling of processes in the root zone of spontaneous vegetation at wet and damp sites in relation to regional water management. In: Hooghart, J.C. (ed.) *Water management in relation to nature, forestry and landscape management.* Proceedings and Information/ TNO Committee on Hydrological Research—The Hague, no. **34**, pp. 91–116.

Kik, C., Jongman, M. & Van Andel, J. (1991): Variation of relative growth rate and survival in ecologically contrasting populations of *Agrostis stolonifera. Plant Species Biol.* **6**: 47–54.

Kleinke, J. (1968): Beschreibung der Moorgrünlandgesellschaften des Mittleren Peenetales. Internal Report EMA Universität Greifswald.

Knapp, E.E. & Rice, K.J. (1996): Genetic structure and gene flow in *Elymus glaucus* (blue wildrye: implications for native grassland restoration. *Rest. Ecol.* **4**: 1–10.

Koerselman, W. & Verhoeven, J.T.A. (1995): Eutrophication of fen ecosystems: external and internal nutrient sources and restoration strategies. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J & Robertson, R.A. (eds): *Restoration of Temperate Wetlands*, pp. 91–112. Wiley, Chichester.

Looijen, R.C. (1995): On the distinction between habitat and niche, and some implications for species' differentiation. *Poznan Studies in the Philosophy of the Sciences and the Humanities* **45**: 87 –108.

Miller, R.S. (1967): Pattern and process in competition. *Adv. Ecol. Res.* **4**: 1–74.

Mohler, C.L. (1983): Effects of sampling pattern on estimation of species distributions along gradients. *Vegetatio* **54**: 97–102.

Mueller-Dombois, D. & Ellenberg, H. (1974): *Aims and Methods of Vegetation Ecology.* Wiley, New York.

Niemann, E. (1973): Grundwasser und Vegetation. *Nova Acta Leopoldina*, No. 6 Suppl. Leipzig.

Noest, V. (1994): A hydrology-vegetation interaction model for predicting the occurrence of plant species in dune slacks. *J. Env. Man.* **40**: 119–128.

Okruszko, H. (1995): Influence of hydrological differentiation of fens on their transformation after dehydration and on possibilities for restoration. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J. & Robertson, R.A. (eds): *Restoration of Temperate Wetlands*, pp. 113–119. Wiley, Chichester.

Scholle, D. & Schhrautzer, J. (1993): Zur Grundwasserdynamik unterschiedlicher Niedermoorgesellschaften Schleswig-Holsteins. *Z. Ökologie u. Natu.* **2**: 87–98.

Ter Braak, C.J.F. & Barendregt, L.G. (1986): Weighted averaging of species indicator values: its efficiency in environmental calibration. *Math. Biosci.* **78**: 57–72.

Ter Braak, C.J.F. & Gremmen, N.J.M. (1987): Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. *Vegetatio* **69**: 79–87.

Ter Braak, C.J.F. & Looman, C.W.N. (1986): Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* **65**: 3–11.

Van der Sluys, P. (1990): Vochtlevering door de grond. In: Locher, W.P. and De Bakker, H. (eds): Bodemkunde van Nederland. Deel 1, Algemene bodemkunde. Malmberg, Den Bosch.

Van Diggelen, R., Grootjans, A.P., Kremmers, R.H., Kooijman, A.M., Succow, M., De Vries, N.P.J. & Van Wirdum, G. (1991a): Hydro-ecological analysis of the fen system Lieper Posse, eastern Germany. *J. Veg. Sci.* **2**: 465–476.

Van Diggelen, R., Grootjans, A.P., Wierda, A., Burkunk, R. & Hoogendoorn, J. (1991b): Prediction of vegetation changes under different hydrological scenarios. In: *Hydrological Basis of Ecologically Sound Management of Soil and Groundwater* (Proceedings of the Vienna Symposium, August 1991). IAHS Publ. no. 202. pp. 71–80.

Wassen, M.J., Van Diggelen, R., Wolejko, L. & Verhoeven, J.T.A. (1996): A comparison of fens in natural and artificial landscapes. *Vegetatio* **126:** 5–26.

Westman, W.E. (1991): Measuring realized niche spaces: climatic response of chaparral and coastal sage scrub. *Ecology* **72:** 1678–1684.

Wheeler, B.D. & Shaw, S.C. (1987): Comparative survey of habitat conditions and management characteristics of herbaceous rich-fen vegetation types. Contract Survey 6, Nature Conservancy Council, Peterborough.

Wierda, A., Fresco, L.F.M., Grootjans, A.P. & Van Diggelen, R. (1997): Numerical assessment of plant species as indicators of groundwater regime. *J. Veg. Sci.* **8:** 707–716.

WRGOD (1978): Regionaal geohydrologisch onderzoek in de provincie. Report. Werkgroep regionaal geohydrologisch onderzoek in de provincie Drenthe.

Zobel, M. (1997): The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.* **12:** 266–269.