Shifts in abundance of fen-meadow species along a nutrient gradient in a field experiment

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Summary

1 Species composition in wetlands depends besides other factors on nutrients levels. Therefore nutrient inputs from adjacent farmland or atmospheric deposition can extend the spatial distribution of species characteristic of nutrient-rich sites, with the potential consequence of excluding species adapted to nutrient-poor conditions. In this study we tested whether wetland species from nutrient-rich and nutrient-poor sites respond in a different way to an experimental nutrient gradient.

2 A two-year fertiliser experiment was set up in spring 1998 in a fen formerly used for agriculture. After the removal of 25 cm of topsoil, 18 common fen meadow species were planted with 18 individuals per species into 10 plots (1 m^2) treated with different amounts of NPK fertiliser: 0–12 g m^{-2} nitrogen, 0–3.9 g m^{-2} phosphorus and 0–23 g m^{-2} potassium. Flowering was recorded during the two growing seasons following planting, while above-ground biomass as well as nutrient concentrations were determined in September 1998 and July 1999.

3 Total biomass production (dry mass) ranged from 600 g m^{-2} (unfertilised plot) to 850 g m^{-2} (addition of $\geq$ 1 g N m^{-2}) in the first year, and from 419 g m^{-2} (unfertilised plot) to 759 g m^{-2} (maximal fertiliser addition) in the second year. Higher rainfall in the second year than in the first led to wetter conditions; the water level differed among plots and strongly affected biomass production.

4 *Carex flava* produced less biomass with increasing fertiliser addition, whereas *Lycopus europaeus, Mentha aquatica* and, in the dry plots, *Selinum carvifolia* responded positively to fertiliser addition. *Centaurea angustifolia, Ranunculus flammula,* and *Silene flos-cuculi* showed maximum biomass production with intermediate fertiliser addition. All species were negatively affected by flood except *M. aquatica* and *R. flammula.*

5 Species from more productive sites tended to benefit more from fertilisation than species from less productive sites, but the difference was not significant. It is concluded that in wetlands, differences in life histories of species and differences in their responses to high water level can play an important role in determining which species will be able to benefit from enhanced nutrient supply

Introduction

The distribution of plant species in wetlands is determined by their physiological performance in dealing with harsh environmental conditions such as anoxia caused by water-logged soil, flooding stress or short nutrient supply (Shaver 1983; Armstrong *et al.* 1994; Weiher *et al.* 1996) and by their ability to compete with each other (Gaudet & Keddy 1995). Interspecific competition generally reduces the distribution of species with respect to environmental conditions and often results in species having optima at different positions along a gradient. Changes in the abundance of species along environmental gradients lead to vegetation patterns that can be regarded as a combination of species response curves (Andrus 1986; Tilman 1987; Bootsma & Wassen 1996; Kotowski *et al.* 1998; but see also Mahdi *et al.* 1989)

Often the effects of environmental conditions and competition interact. Thus, changes in nutrient availability can affect the competitive balance of plant species with different resource requirements. When grown in monoculture, even species from nutrient-poor sites generally increase their biomass production with enhanced fertiliser supply (e.g. McGraw & Chapin 1989), but in mixed swards the same species may be reduced by fertilisation due to impairment of light conditions (e.g. Twolan Strutt & Keddy 1996; Pauli 1998; Wetzel & van der Valk 1998; Leps 1999). Therefore, vegetation change due to nutrient enrichment results in the loss of small, slow-growing, rare species adapted to nutrient-poor conditions (e.g. Landolt 1991; Ellenberg 1985).

Effects of nutrient enrichment on species composition can be directly observed in wetlands bordered by farmland. From the border zone, tall forb species and tall grasses (e.g. *Phragmites australis*) penetrate into the sedge- or *Molinia*-dominated plant communities, building a narrow or extended zone of mixed communities (Boller-Elmer 1977; Zelesny 1994). Thus, wetland border zones tend to constitute a steep environmental gradient along which plant species show different response curves (Zelesny 1994; Güsewell & Klötzli 1998). Some species are mostly restricted to a certain position along the gradient, whereas others are found over wide distances with changing abundance and vitality (Zelesny 1994). It is frequently observed that tall forb borders expand (Klötzli 1979). Since seedling establishment is of reduced importance compared to vegetative dispersal in wetlands (Oomes & van der Werf 1996; Jensen 1997; Jauhiainen 1998), the expansion of tall forb borders is primarily effected by species already present in the fen meadows, though small of stature and not reproducing (e.g. de Swart *et al.* 1994).

To gain a better understanding of processes causing vegetation change in wetland border zones we investigated the following questions in a field experiment:

- How does the abundance of different wetland species change along a nutrient gradient?
- Which is the minimal amount of nutrient addition causing marked shifts in species performances – can a "critical load" be defined?
- Are species responses in the experiment related to their distribution along nutrient gradients in the field?

The aim of this paper is to evaluate the biomass production of species grown under competition at enhanced nutrient supply and to compare the species' responses in the experiment with their occurrence in fen meadows.

Methods

EXPERIMENTAL DESIGN AND PLANT MATERIAL

A field experiment was set up in a fen drained in 1943 and used for agricultural production until 1995 near Hüttwilersee (Canton Thurgau, North Eastern Switzerland). In early spring 1998, ten plots of 1.2 m x 1.2 m were arranged in two rows with a strip of 1 m between them. To reduce the nutrient load of the soil (high due to former agricultural use, cf. Sharpley 1995; Patzelt & Pfadenhauer 1998), and to increase the water level, topsoil was removed to a depth of 25 cm below the soil surface. In spring 1999, plots were surrounded by corrugated plastic sheets to fortify the walls and to prevent disturbance by mice.

Eighteen wetland species from Central Europe were used for the experiment: *Anthoxanthum odoratum* L., *Carex elata* All., *Carex flava* L., *Centaurea angustifolia* Schrank, *Cirsium palustre* (L.)Scop., *Filipendula ulmaria* (L.)Maxim., *Hypericum perforatum* L., *Lycopus europaeus* L., *Lysimachia vulgaris* L., *Lythrum salicaria* L., *Mentha aquatica* L., *Molinia coerulea* (L.)Moench, *Primula farinosa* L., *Ranunculus flammula* L., *Schoenus* sp., *Selinum carvifolia* L., *Silene flos-cuculi* (L.)Clairv., *Succisa pratensis* Moench. Plants were grown from seeds collected in fen meadows not further than 15 km from the experimental area in 1996/97 (except *A. odoratum:* obtained from UFA seeds, Winterthur, origin unknown). Seeds of some species were pre-treated to promote germination following the recommendations of Maas (1989), and all species were sown on 11 March 1998 in the greenhouse. Seedlings were transplanted into the experimental plots on 3–4 June 1998. Leaving a border of 10 cm, 18 individuals of each of the 18 wetland species were planted into each plot in a Latin square design. See Bollens (2000) for details. Nomenclature follows Hess *et al.* (1991)

FERTILISER TREATMENTS

The ten plots were randomly attributed to nine fertilisation treatments (different additions of fertiliser) and one control treatment (no fertilisation). In the treatment with maximal fertilisation, nutrients were added in the amounts recommended for meadows mown five times per year, i.e. 12 g m^{-2} nitrogen, 3.9 g m^{-2} phosphorus and 23 g m^{-2} potassium (Wirz-Kalender 1995). In the other treatments, these amounts were reduced following a geometric series with successive levels differing by a factor of 0.6 in the first year and 0.5 in the second year. Thus, the lowest level of addition was 0.2 g N m^{-2} a^{-1} in the first year and 0.047 g N m^{-2} a^{-1} in the second year. P and K were supplied in amounts proportional to those of N, so that N:P = 3 and N:K = 0.5 in all treatments.

A basic nutrient solution was produced by dissolving 6.46 g KH_2PO_4, 17.76 g KNO_3 and 21.41 $Ca(NO_3)_2 \cdot 4H_2O$ in 1 l distilled Water, resulting in 5 g N, 1.5 g P, 8.7 g K and 3.6 g Ca per litre. For fertiliser application, the appropriate amount of nutrient solution was diluted with 5 l of deionised water (in dry periods) or poured directly into the standing water when plots were flooded. In the first case the same amount of water was added to the control plot. Fertiliser was applied bi-weekly from mid-June to mid-September 1998 (7 applications) and from early April to the end of June 1999 (6 applications).

HARVEST AND MEASUREMENTS

Plants were harvested on 7–10 September 1998 and on 5–8 July 1999 by clipping 4 cm above soil surface. All individuals of one species per plot were pooled. Plants were dried at 60 °C and weighed. Total N and P concentra-

tion in dried plant material was determined by Kjeldahl digestion followed by colorimetric analysis. *P. farinosa* and *S. pratensis* rosettes and a few individuals of other species severely weakened due to herbivory or partial putrescence were not harvested in the first season to ensure survival.

As a measure of reproductive effort, 'flower units' were counted either bi-weekly (short-lived inflorescences of *R. flammula* and *S. flos-cuculi*) or once at the time of harvesting (other species). "Flower units" were single flowers (*R. flammula, S. flos-cuculi*), capitulae (*C.*

angustifolia, C. palustre), ears (*A. odoratum, C. elata, C. flava, M. coerulea, M. aquatica*) or flowering shoots (*L. europaeus, L. salicaria*).

The mean water level was recorded during the second growing season (measured bi-weekly at three points within each plot) because extraordinarily wet weather conditions caused experimental plots to be flooded from the end of March to June 1999.

SPECIES DISTRIBUTION IN THE FIELD

To compare species responses to nutrient supply under experimental conditions with
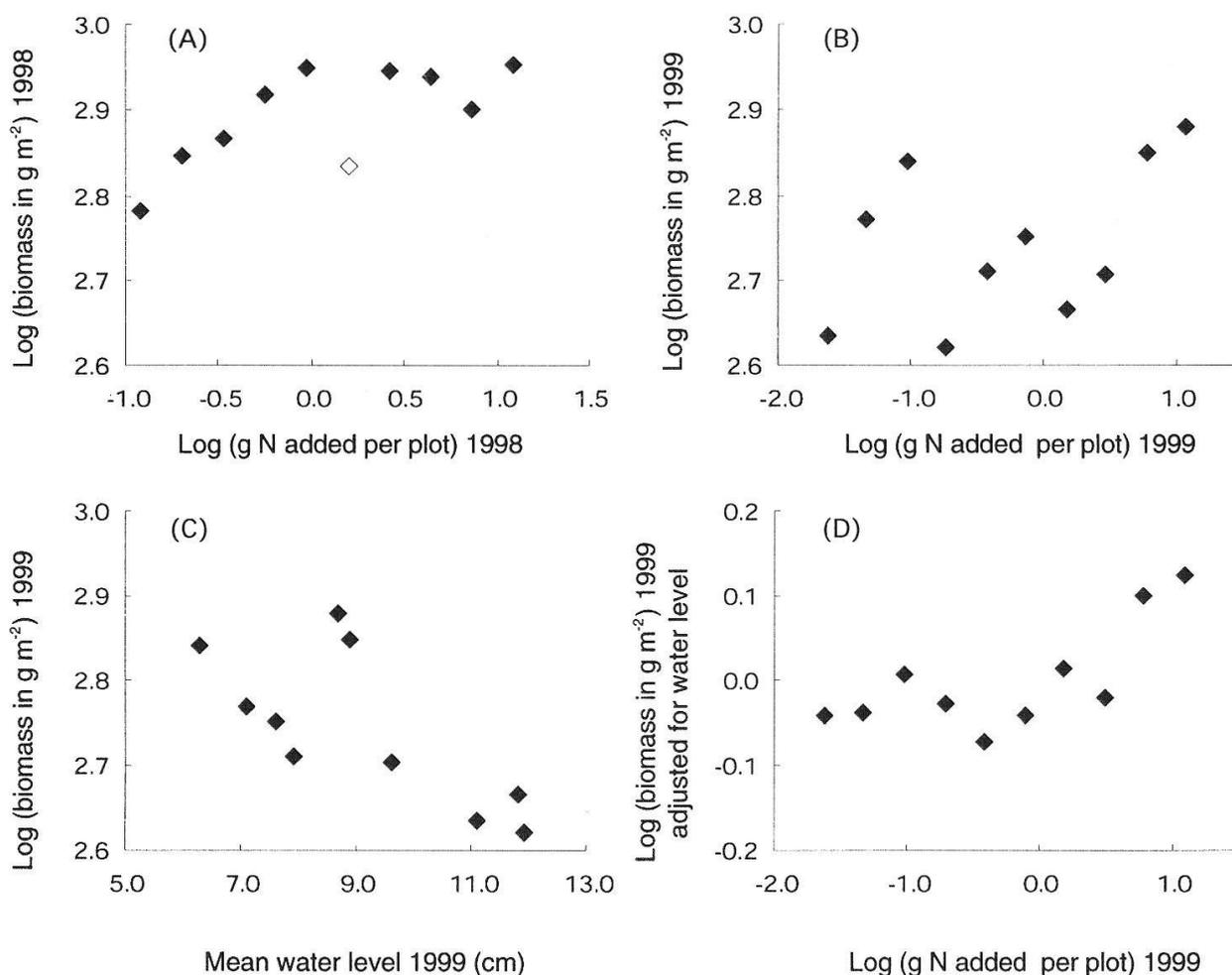
Fig. 1. Total above-ground biomass of the experimental plots (A) at the first harvest (1998) and (B–D) at the second harvest (1999) in relation to nutrient and water level. Nutrient levels are represented by the amount of N added; P addition was 1/3 of this amount, and K addition was 2 x this amount. Mean water level 1999 in (C) is the mean of bi-weekly measurements during the growing season 1999, expressed in cm above soil surface. In (D) above-ground biomass 1999 was adjusted for water level by subtracting from original biomass values the variation explained by water level.

Table 1. Standardised regression coefficients and significance of the linear regression of log-transformed biomass $(g\ m^{-2})$ against fertiliser addition $(g\ N\ m^{-2}\ a^{-1}$, log-transformed) or water level in 1998 (first year) and in 1999 (second year); *= P < 0.05; *= P < 0.01; ***= P < 0.001

Species	1998 fertiliser	1999 fertiliser	1999 water
Anthoxanthum odoratum	0.25	0.21	-0.84 **
Carex elata	-0.07	-0.54	-0.59
Carex flava	0.44	-0.52	-0.74 *
Centaurea angustifolia	-0.14	0.08	-0.88 ***
Cirsium palustre	-0.41	0.33	-0.31
Filipendula ulmaria	0.11	0.20	-0.80 **
Lycopus europaeus	0.67*	0.87**	-0.12
Lysimachia vulgaris	0.14	0.18	-0.01
Lythrum salicaria	0.05	0.46	-0.54
Mentha aquatica	0.55	0.90 ***	0.06
Molinia coerulea	-0.53	-0.55	-0.69*
Ranunculus flammula	-0.70 *	-0.22	0.29
Selinum carvifolia	0.94 ***	0.31	-0.58
Silene flos-cuculi	0.27	0.09	-0.79 **

their occurrence in wetlands, vegetation surveys were performed in 10 wetlands in Canton Zürich in August 1998 or July 1999. For details see Bollens (2000, p. 103). The wetlands contained various vegetation types (phytosociological alliances Magnocaricion, Caricion davallianae, Filipendulion and Molinion). In all wetlands transects were laid from a eutrophicated border zone with Filipendulion towards the less productive centre of the wetland. The vegetation was surveyed in 5-8 plots per transect on an area of $2 \times 2\ m^2$ according to Braun-Blanquet. As a measure of site productivity, the above-ground biomass of each plot was harvested in two subplots of $20 \times 80\ cm^2$, dried at 70 °C and weighed. Each species' optimum along the nutrient gradients was quantified by weighted averaging (ter Braak & Looman 1986). *P. farinosa* was not present at the surveyed sites.

DATA ANALYSIS

Most data were log-transformed for statistical analysis. For biomass data, the transformation $\log_{(y+1)}$ was used, and for nutrient concentrations, $\log_c$. Flower counts were not transformed. Levels of fertilisation were transformed to a linear scale (with equal increments between successive levels) through log-transformation of nitrogen supply ($\log_N$) and extrapolation for control plots. To investigate the relationship between biomass production and nutrient addition or water level for each species, we first fitted quadratic regression models and then linear models if the quadratic term was not significant. These analyses were carried out with the statistical package JMP 3.2 (SAS Institute Inc. 1989).

Results

VEGETATION STRUCTURE AND SPECIES COMPOSITION

Plant growth was high in the first year (1998), with plots reaching cumulated cover values above 100%, except in the unfertilised control. *L. europaeus* was the dominant species followed by *L. salicaria* and *A. odoratum*.
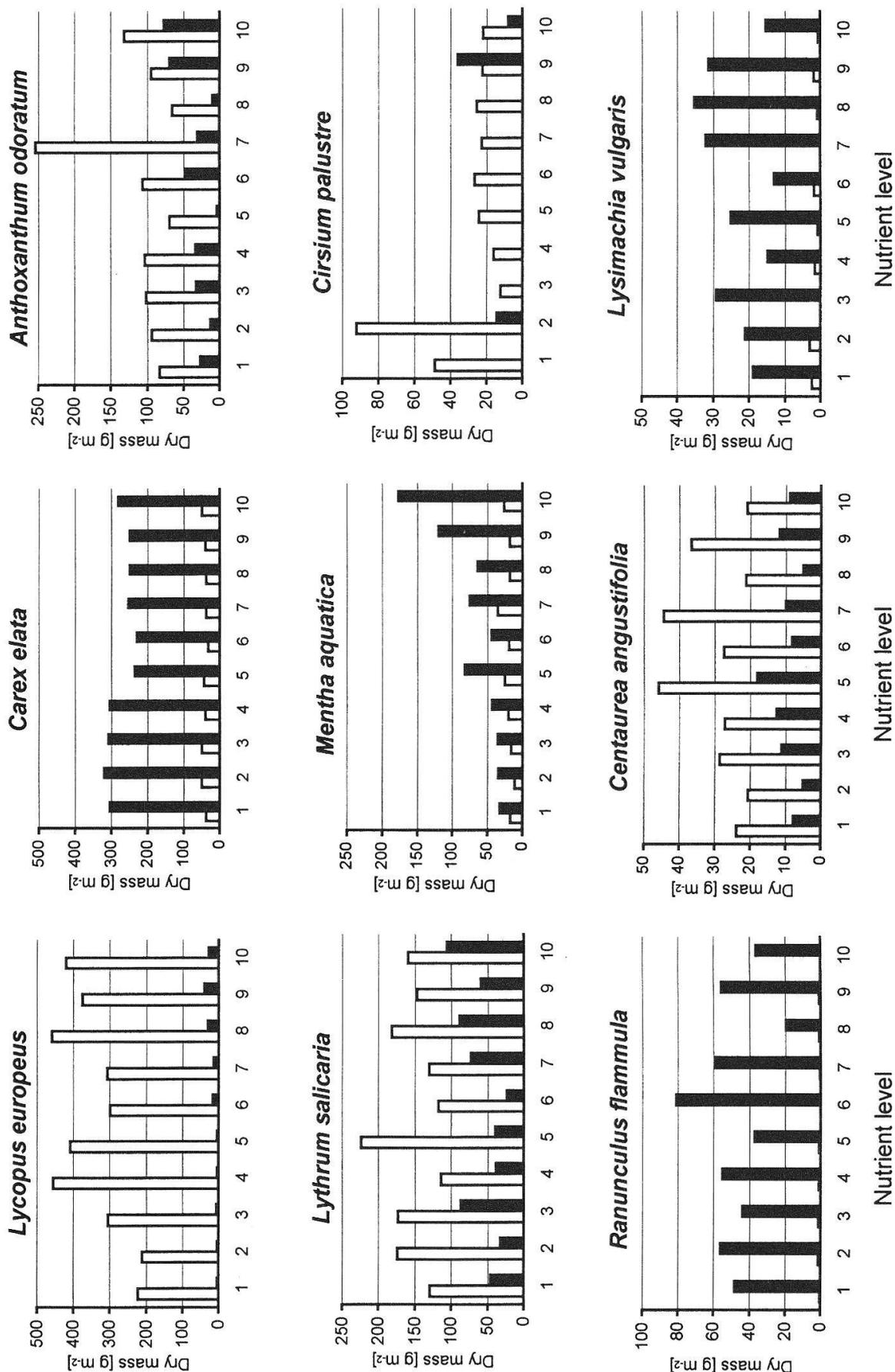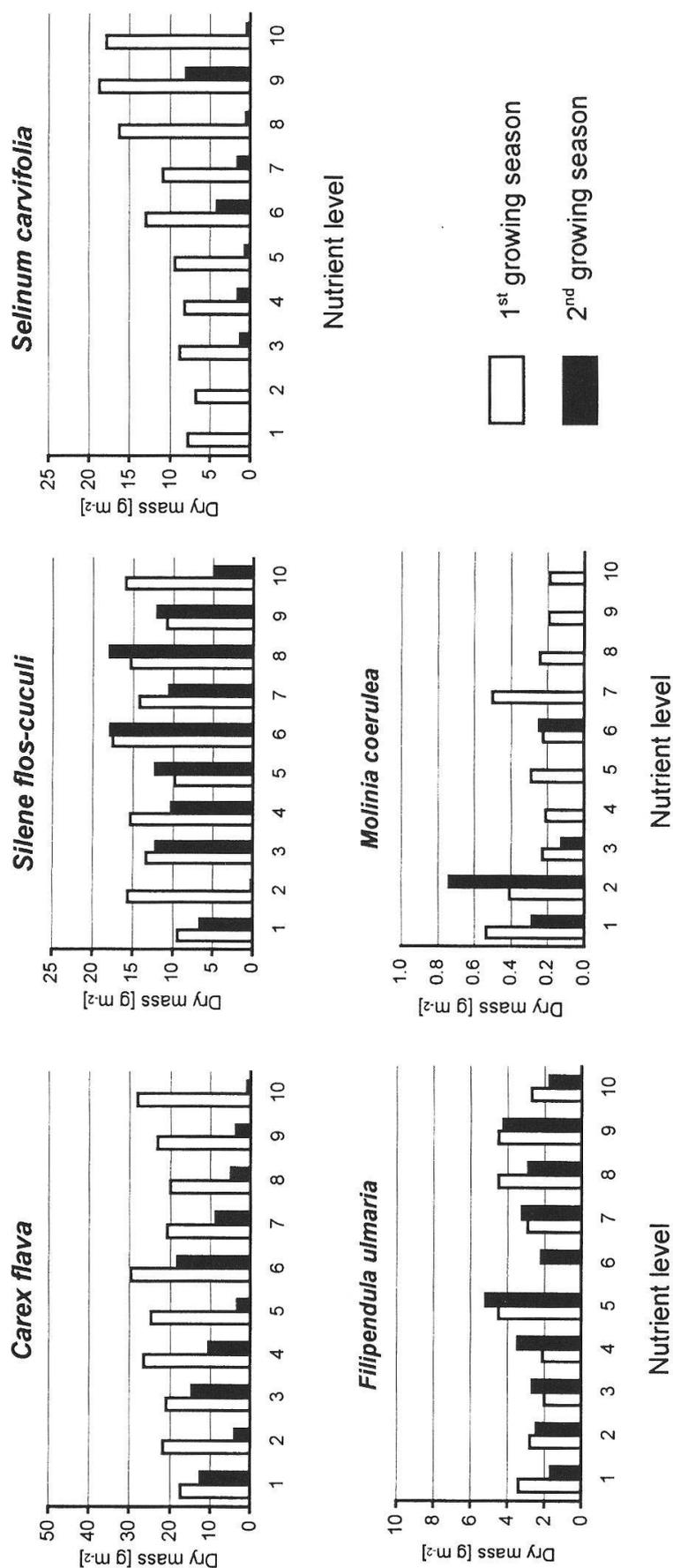
Fig. 2. Biomass production of individual species in relation to nutrient and water level in the two growing seasons. The effect of water level in the second growing season was eliminated by subtracting from original biomass values the variance explained by the water level. Nutrient levels are coded as 1, no nutrients added; 2, lowest amount of nutrients added ... 10, highest amount of nutrients added; see text or Fig. 1 for exact amounts. The scale of y-axes differs among species.

Table 2. Standardised regression coefficients and significance of the linear regression of the number of flower units against fertiliser addition (g N m^{-2} a^{-1}) or water level in 1998 (first year) and in 1999 (second year); * = P < 0.05; * = P < 0.01; *** = P < 0.001

Species	1998	1999	
	fertiliser	fertiliser	water
Centaurea angustifolia	0.04	-0.32	-0.83 ***
Carex elata		-0.30	0.00
Carex flava		-0.67 *	-0.55
Lycopus europaeus	0.29		
Lythrum salicaria	0.05		
Mentha aquatica	-0.34		
Molinia coerulea	-0.24		
Ranunculus flammula	0.22	-0.07	-0.32
Silene flos-cuculi	0.72 *	0.03	-0.80 ***

In the second year (1999), plots were dominated by *A. odoratum* in early spring and by *C. elata* tussocks at harvest time. Three species (*H. perforatum, Schoenus* sp., *P. farinosa*) could no longer be found at the end of the second growing season, and two species (*M. coerulea* and *S. pratensis*) only remained as a few small specimens. *C. palustre* also occurred only in small numbers but some individuals were very tall and even produced flowers.

ABOVE-GROUND BIOMASS

Total above-ground biomass production in the first year (1998) ranged from 602 to 896 g m^{-2} (dry mass). It increased gradually from 600 g m^{-2} (unfertilised control) to 891 g m^{-2} (supply of 1 g N m^{-2}) and then levelled off (Fig. 1A). Total biomass at nutrient level 6 was particularly low, which could not be explained by a higher loss of individuals from productive species or higher mice activity, nor by lower nutrient supply reflected in extractable soil nutrients after harvest. Thus, this quadrat was treated as an outlier and excluded from data analysis.

In the second year (1999), high water levels inhibited biomass production considerably. Total biomass production was therefore lower than in the first year, with values between 419 and 759 g m^{-2} (Fig. 1B), and it was negatively related to the mean water level measured in the plots in spring 1999 (Fig. 1C). If biomass production was adjusted for differences in the degree of flooding (using the residuals of a linear regression of biomass against mean water level), a positive relationship with fertilisation addition was found (Fig. 1D). However, in contrast to 1998, this positive relationship was mostly due to the two plots with highest fertiliser addition having higher biomass than the others (Fig. 1D).

Only a few species responded clearly to fertiliser addition (Fig. 2). In the first year, *L. europaeus* and *S. carvifolia* increased biomass with increased fertiliser addition, whereas *R. flammula* decreased (Table 1). In the second year, *M. aquatica* and *L. europaeus* increased biomass with increased nutrients whereas *M. coerulea* and *C. flava* tended to decrease (but not significantly). Quadratic regressions (testing for a unimodal dependence of biomass

production on nutrient supply) were not significant for any of the species, though *C. angustifolia* and *M. aquatica* (only first year) tended to produce maximal biomass around nutrients levels 5 and 7, respectively.

BIOMASS NUTRIENT CONCENTRATIONS

Nutrient export by harvesting ranged from 16 to 23 g N m^{-2} and from 1.8 to 2.7 g P m^{-2} in the first year and correlated well with nutrient addition (for N: $r^2 = 0.56$, $P < 0.05$; for P: $r^2 = 0.83$, $P < 0.001$). Results for the second year were similar, although the export of N was lower than in the first year (6 to 11 g N m^{-2}, 1.5 to 3.8 g P m^{-2}).

Nitrogen concentration in plants (all species pooled) ranged from 24 to 26 mg g^{-1} in the first year and from 13 to 16 mg g^{-1} in the second year. In the first year, nitrogen concentration was not significantly related to fertiliser addition (Fig. 3A), whereas in the second year, fertiliser addition had a slight positive effect on nitrogen concentration (Fig. 3B). Mean phosphorus concentrations in plants ranged from 2.6 to 3.4 mg g^{-1} in the first year and from 3.2 to 5.0 mg g^{-1} in the second year.
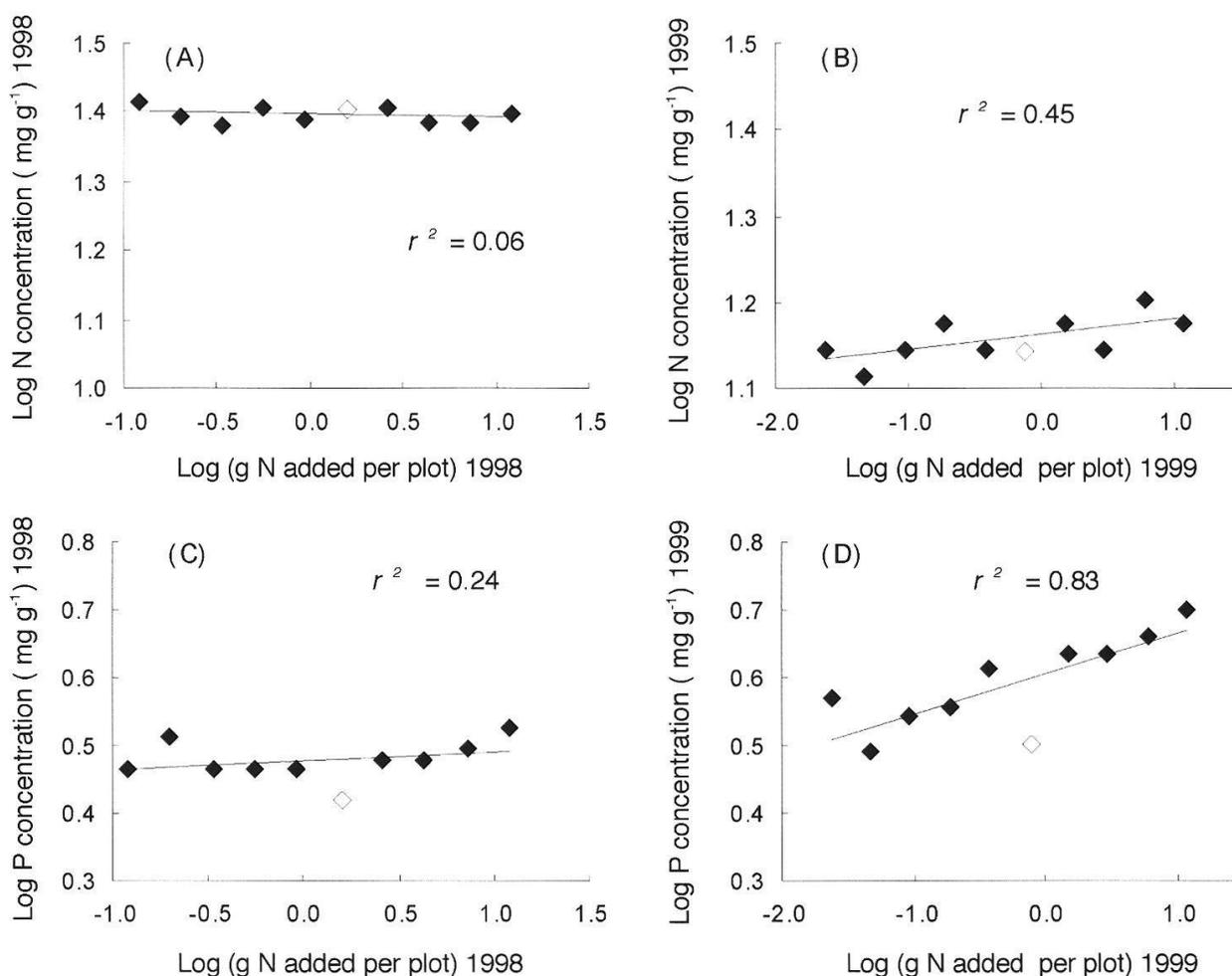
Fig. 3. Nutrient concentrations (A, B: nitrogen; C, D: phosphorus) in the above-ground biomass of experimental plots (all species pooled) in relation to NPK-fertiliser addition (A, C) in 1998 and (B, D) in 1999. Fertiliser levels were represented by the amount of N added; P addition was 1/3 of this amount. Coefficients of determination of linear regression shown in graphs were calculated without fertiliser level 6 (white symbols) since the latter was an obvious outlier (cf. Fig. 1A)

In both years, plant phosphorus concentration responded positively to fertiliser addition, if the outlier (fertiliser level 6) was excluded, but the relationship was only significant in the second year (Fig. 3C,D).

The stronger response of phosphorus concentration than of nitrogen concentration led to a decline in N:P ratios with enhanced fertiliser supply in both years (from 8.9 to 7.4 in the first year and from 4.0 to 2.9 in the second year). Neither nutrient concentrations nor N:P ratios depended on the water table.

FLOWERING

In the first year *L. europaeus, L. salicaria, R. flammula, S. flos-cuculi, C. angustifolia* and, sporadically, *M. coerulea* and *M. aquatica* expressed flowers (the latter species were excluded from statistical analyses). Production of flower units was significantly positively correlated with nutrient addition for *S. flos-cuculi* (Table 2). No significant effect of nutrient addition could be detected for the other species.

In the second year seven species produced flowers. *A. odoratum* started with flower production in early spring. Ears were not counted exactly, but it was obvious that there were many more inflorescences in the five drier plots than in the heavier flooded ones (ca. 450 m^{-2} vs. 50 m^{-2}). *C. palustre* produced flowers only in the plot with fertiliser level 1, 2 and 9 (42/154/2 capitulae, respectively). These species were not included in statistical analysis. In three of the other species, nutrient addition or water level significantly affected flower production (Table 2). High nutrient levels generally led to lower numbers of flower units in 1999 (contrary to 1998), especially for *C. flava*. All species except *C. elata* (with ≤ 2 flower units per plot, so that data are not very reliable), produced distinctly fewer flowers at high water levels.

RESPONSES COMPARED TO SPECIES DISTRIBUTION IN THE FIELD

The species used in the experiment clearly differed in their distribution along nutrient gradients in the field. *Carex flava, Ranunculus flammula* and *Lycopus europaeus* occurred mostly at low-productive sites (weighted average above-ground biomass < 300 g m^{-2}). *Filipendula ulmaria, Lysimachia vulgaris* and *Anthoxanthum odoratum* occurred at the most productive sites (weighted average above-ground biomass > 350 g m^{-2}).

To compare the occurrence of the species along nutrient gradients in the field with the effect of nutrient addition, this effect was calculated by dividing biomass in the lowest fertilised plot by biomass in the second highest. These two plots were used for the calculation because they were situated in the drier line of plots, so that results based on them would be less affected by differences in water level. Species from more productive habitats (weighted average biomass > 325 g m^{-2}) tended to respond more strongly to fertilisation (biomass enhanced by 48% in 1998, and by 67% in 1999) than species from less productive habitats (+24% in 1998, +31% in 1999) but the means did not differ significantly.

Discussion

LIFE HISTORIES AND GROWTH STRATEGIES AS DETERMINANTS OF SPECIES RESPONSES TO FERTILISATION

In this experiment all species survived during the first growing season, but several had disappeared by the end of the second growing season. The same 18 species as used in this study were grown in a pot experiment without competition under restricted nutrient supply (Bollens 2000). All of them developed well (with the exception of *H. perforatum*). Therefore it can be assumed that in the field

experiment *Schoenus* sp. and *P. farinosa*, both being small-growing species, were inhibited mostly by light or space competition. *P. farinosa* is known to establish only successfully where gaps loosen the vegetation (Maas 1988).

Some species like *L. europaeus, L. salicaria* and *A. odoratum* grew very fast and obtained high biomass in the first year. At higher fertilisation levels the individuals of these highly productive species interacted: *A. odoratum* reached its maximum (50%) at level 4 where both *L. europaeus* and *L. salicaria* had a minimum in percentage of total biomass. In plots with a high biomass of *L. europaeus* and *L. salicaria,* the biomass of *A. odoratum* was relatively smaller. The interaction between the three species was reflected in the constant percentage of total biomass they occupied, which was around 80% at high nutrient levels. The increase of one species when another species was harmed was found to be a process in stabilising community biomass production (Tilman 1996). In our experiment, different species had an advantage when highly productive species (*A. odoratum, C. angustifolia, M. aquatica* and *M. coerulea*) were impaired.

In contrast to the fast-growing species, slower-growing but potentially tall species, such as *C. elata* and *L. vulgaris,* had higher biomass in the second season compared to the first. Although production was generally lower in the second year *L. vulgaris* and *C. elata* increased total biomass 16- and 7-fold, respectively, compared to the first year. *C. elata* contributed less than 10% to total aboveground biomass in the first year but produced between 36% and 65% of total biomass in the second year. Because *C. elata* grew better in the drier plots, it is unlikely that the water factor produced this change in dominance. *C. elata* was clearly discriminated by growing

slowly in the starting phase of the experiment, but immediately after the first harvest, the plants displayed a compensatory growth response. The tussocks produced new leaves, and even during the hot, dry late summer 1999 they tended to dominate. In contrast, *L. europaeus,* which dominated until the first harvest, did not show a compensatory growth response. Although this species can be found in areas flooded annually, as well as on waterlogged soils (Neuhäuslova 1979) the percentage of biomass produced did not exceed 6% in the second season.

R. flammula and *M. aquatica* also increased their biomass between the first and the second year, but probably for other reasons than *C. elata* and *L. vulgaris. R. flammula* and *M. aquatica* produced less than 5% of total biomass in the first year. In the second year the sward was more open due to inundation, and these species reached light and escaped flooding by producing runners and branches dispersed in all directions. *R. flammula* is a successful stress tolerator at nutrient-poor sites controlled by flooding (Day *et al.* 1988). However, it displays a certain "guerrilla" strategy, being able to act as a pioneer, colonising disturbed spots (Grootjans & Ten Klooster 1980; M. Peintinger, *pers. comm.,* Bollens 2000). Rosette plants do not display this "guerrilla" strategy.

The experimental field had relatively high nutrient levels even though topsoil had been removed. Compared to other wetlands both phosphorus and nitrogen contents in the soil were high (Bollens 2000). During winter, when no fertiliser was applied, nutrients were incorporated by the vegetation and/or leached, and in the following spring soil nutrients showed intermediate supply. The naturally high nutrient supply enabled species from medium-rich stands (Landolt nutrient indicator value 3) to dominate even the unfertilised

control. With the exception of *R. flammula* in the second year, species of poor soils (Landolt nutrient indicator value of 2) never produced more than 5% of total biomass. Nutrient concentrations in above-ground biomass also indicated a sufficient nutrient supply. Both nitrogen and phosphorus concentrations, even in the control plot, were higher than in natural wetlands (e.g. Sackriet; Bollens 2000) and far above the critical values (de Wit *et al.* 1963). In the first year, additional nitrogen was transferred into additional plant biomass and plant tissue concentrations were the same under all treatments. In autumn, soil nutrient concentrations indicated a nutrient surplus. Contrary to nitrogen, phosphorus concentrations increased with enhanced fertiliser addition and indicated a luxury consumption of that nutrient. In the second year, nitrogen concentration also increased with additional fertiliser supply which is consistent with the findings of Vermeer (1986).

EFFECTS OF FERTILISER ADDITION

In the first year, most species increased in biomass with fertiliser addition from 2 kg N ha^{-1} a^{-1} + 0.7 kg P ha^{-1} a^{-1} up to an addition of 10 kg N ha^{-1} a^{-1} + 3 kg P ha^{-1} a^{-1}. Field fertiliser experiments performed by Kirkham *et al.* (1996) showed that small increases in soil fertility (25 kg N ha^{-1} a^{-1} + P) lead to significant changes in the composition of the plant community.

Biomass production in European wetlands is mostly limited by nitrogen or phosphorus (Aerts *et al.* 1992; Verhoeven *et al.* 1996; Wassen & Joosten 1996; Boeye *et al.* 1997; Pauli 1998). Potassium limitation is observed rarely (Egloff 1983; Zelesny 1994; van Duren *et al.* 1997). At our sites the low N:P ratios in control plots (< 10) suggested limitation by nitrogen (Koerselman & Meuleman 1996). However, the nature of limitation can change

with the successional stage (Koerselman & Verhoeven 1992; Olff & Pegtel 1994), atmospheric N deposition (Aerts *et al.* 1992; Verhoeven *et al.* 1996), or changes in management (Kirkham *et al.* 1996). Because of the small amounts of fertiliser that can cause changes in productivity and induce vegetation change (Kirkham et al. 1996) and because there is no general pattern for nutrient limitation, in our opinion the "critical loads" approach (e.g. Bull 1992) is not applicable for European wetlands. An input of 20–35 kg N ha^{-1} a^{-1} as mentioned by Bobbink & Roelofs (1995) causes biomass enhancement according to our first-year results. Admittedly, we have to consider that we added not only nitrogen but also phosphorus, which might have led to a stronger response than nitrogen alone, and that the response of seedlings, as planted in this experiment, may differ from the response of established stands of vegetation. Indeed, in the second year of our experiment, biomass was only enhanced by the higher levels of fertilisation.

EFFECTS OF FLOODING

Most species survived the long-lasting deep flooding during the second growing period of this experiment, which is consistent with other investigations (Peintinger 1990; Lenssen *et al.* 1998). Flooding affected both biomass production and flower expression. Reduced fitness regarding production of inflorescences due to inundation was observed likewise by Peintinger (1990). Rosette species and grasses were obviously more strongly affected than other species. Water level was the most important factor inhibiting biomass production in the second year, and dominance was obtained by species originating from wet, water-soaked habitats (*C. elata* and *M. aquatica*). Even *R. flammula*, a species from nutrient-poor but wet sites, could produce a

considerable percentage of total biomass in the second year (up to 15%). By contrast, tall forbs are known to be inhibited by inundation (Lenssen *et al.* 1998). In this experiment *C. angustifolia, F. ulmaria* and *S. flos-cuculi* were severely affected by flooding even at the highest levels of fertilisation. Thus, under sufficiently wet conditions eutrophication would not lead to the formation of tall forb stands.

RESPONSES IN THE EXPERIMENT
COMPARED TO SPECIES DISTRIBUTION IN
THE FIELD

We had hypothesised that species from more productive sites would respond more strongly to fertiliser addition, since such a difference in response has been observed in laboratory experiments comparing the growth of species from different habitats at high and low nutrient supply (e.g. Fichtner & Schulze 1992; Elberse & Berendse 1993; Garnier 1998). This difference has been used to explain shifts in species composition occurring after eutrophication: species that are able to benefit most from higher nutrient supply would become dominant. In our experiment, the expected difference in response to fertiliser was found as a tendency when species were subdivided in two groups according to the productivity of their sites (<325 g m^{-2} and >325 g m^{-2}), but this was not significant. If we assume that our hypothesis was basically correct, there may be three reasons for this lack of significance. First, even the plot with lowest level of fertiliser addition was rather productive due to the high nutrient content of the unfertilised soil. Thus, our experiment considered a different range of nutrient conditions than the conditions prevailing at the investigated field sites. Second, the long-term response of species to low, but continued nutrient inputs may differ considerably from their response in a short-term experiment where plants are grown from seedlings. Third,

the ability of species to respond to nutrient addition may have been influenced by the high water level in the second year. In conclusion, our experiment has suggested that different responses to nutrient addition may be an important factor in vegetation change caused by eutrophication, but that in wetlands differences in life histories and differences in response to high water level can play an important role in determining which species will be able to benefit from enhanced nutrient supply.

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References

Aerts, R., Wallén, B. & Malmer, N. (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subjected to low and high atmospheric nitrogen supply. *Journal of Ecology,* **80,** 131–140.

Andrus, R. E. (1986) Some Aspects of Sphagnum Ecology. *Canadian Journal of Botany,* **64,** 416–426.

Armstrong, W., Brändle, R. & Jackson, M.B. (1994) Mechanisms of flood tolerance in plants. *Acta Botanica Neerlandica,* **43,** 307–358.

Bobbink, R. & Roelofs, J. G. M. (1995) Nitrogen critical loads for natural and semi-natural ecosystems: The empirical approach. *Water Air and Soil Pollution,* **85,** 2413–2418.

Boeye, D., Verhagen, B., Van Haesebroeck, V. & Verheyen, R. F. (1997) Nutrient limitation in species-rich lowland fens. *Journal of Vegetation Science,* **8,** 415–424.

Bollens, U. (2000) E*ffects of nutrients inputs and water regime on wetland vegetation and the performance of wetland species.* Dissertation ETH Zürich, No. 13560, 145 p.

Boller-Elmer, K. C. (1977) Stickstoff-Düngungs-einflüsse von Intensiv-Grünland auf Streu- und Moorwiesen. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich,* 63, 1–103.

Bootsma, M. C. & Wassen, M. J. (1996) Environmental conditions and fen vegetation in three lowland mires. *Vegetatio,* 127, 173–189.

Bull, K. R. (1992) An introduction to critical loads. *Environmental Pollution,* 77, 173–176.

Day, R. T., Keddy, P. A., McNeil, J. & Carleton, T. (1988) Fertility and disturbance gradients: A summary model for riverine marsh vegetation. *Ecology,* 69, 1044–1054.

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

De Wit, C. T., Dijkshoorn, W. & Noggle, J. E. (1963) Ionic balance and growth of plants. *Verslagen van landbouwkundige Onderzoekingen,* 69.

Egloff, T. B. (1983) Der Phosphor als primär limitierender Nährstoff in Streuwiesen (Molinion). Düngungsexperiment im unteren Reusstal. *Berichte des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich,* 50, 119–148.

Ellenberg, H., Jun (1985) Veränderungen der Flora Mitteleuropas unter dem Einfluss von Düngung und Immissionen. *Schweizerische Zeitschrift für das Forstwesen,* 136, 19–39.

Fichtner, K. & Schulze, E.-D. (1992) The effect of nitrogen nutrition on growth and biomass partitioning of annual plants originating from habitats of different nitrogen availability. *Oecologia,* 92, 236–241.

Garnier, E. (1998) Interspecific variation in plasticity of grasses in response to nitrogen supply. *Population Biology of Grasses* (eds. G.P. Cheplick), pp. 155–181. Cambridge University Press, Cambridge.

Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology,* 76, 280–291.

Grootjans, A. P. & Ten Klooster, W. P. (1980) Changes of groundwater regime in wet meadows. *Acta Botanica Neerlandica,* 29, 541–554.

Güsewell, S. & Klötzli, F. (1998) Abundance of common reed (*Phragmites australis*), site conditions and conservation value of fen meadows in Switzerland. *Acta Botanica Neerlandica,* 47, 113–129.

Hess, H. E., Landolt, E. & Hirzel, R. (1991) *Bestimmungsschlüssel zur Flora der Schweiz und angrenzender Gebiete.* 3rd ed., Birkhäuser, Basel. 3 Vol., 858, 956, 876 pp.

Jauhiainen, S. (1998) Seed and spore banks of two boreal mires. *Annales botanici Fennici,* 35, 197–201.

Jensen, K. (1997) Ecological studies of vegetation in nutrient-rich abandoned wet meadows: Successional sere and dynamic behaviour of individual species. *Feddes Repertorium,* 108, 603–625.

Kirkham, F. W., Mountford, J. O. & Wilkins, R. J. (1996) The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. *Journal of Applied Ecology,* 33, 1013–1029.

Klötzli, F. (1979) Ursachen für Verschwinden und Umwandlung von Molinion-Gesellschaften in der Schweiz. *Werden und Vergehen von Pflanzengesellschaften* (eds O. Wilmanns & R. Tüxen), pp. 451–467. J. Cramer, Vaduz.

Koerselman, W. & Verhoeven, J. T. A. (1992) Nutrient dynamics in mires of various trophic status: nutrient inputs and outputs and the internal nutrient cycle. *Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation.* (ed. J. T. A. Verhoeven), pp. 397–432. Kluwer Academic Publishers, Dordrecht.

Koerselman, W. & Meuleman, A.F.M. (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology,* 33, 1441–1450.

Kotowski, W., Van Diggelen, R. & Kleinke, J. (1998) Behaviour of wetland plant species along a moisture gradient in two geographically distant areas. *Acta Botanica Neerlandica,* 47, 337–349.

Landolt, E. (1991) *Gefährdung der Farn- und Blütenpflanzen in der Schweiz mit gesamtschweizerischen und regionalen roten Listen.* BUWAL, Bern.

Lenssen, J. P. M., Ten Dolle, G. E. & Blom, C. W. P. M. (1998) The effect of flooding on the recruitment of reed marsh and tall forb plant species. *Plant Ecology,* 139, 13–23.

Leps, J. (1999) Nutrient status, disturbance and competition: An experimental test of relation-

ships in a wet meadow copy. *Journal of Vegetation Science,* **10,** 219–230.

Maas, D. (1988) Keimung und Etablierung von Streuwiesenpflanzen nach experimenteller Ansaat. *Natur und Landschaft,* **63,** 411–415.

Maas, D. (1989) Germination characteristics of some plant species from calcareous fens in southern West Germany and their implications for the seed bank. *Holarctic Ecology,* **12,** 337–344.

Mahdi, A., Law, R. & Willis, A. J. (1989) Large niche overlaps among coexisting plant species in a limestone grassland community. *Journal of Ecology,* **77,** 386–400.

McGraw, J. B. & Chapin, F. S., III (1989) Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology,* **70,** 736–749.

Müller, J., Rosenthal, G. & Uchtmann, H. (1992) Vegetationsveränderungen und Ökologie nordwestdeutscher Feuchtgrünlandbrachen. *Tuexenia,* **12,** 223–244.

Neuhäuslova, Z. (1979) *Pruno-Fraxinetum* in the Czech Socialist Republic, Czechoslovakia. *Folia Geobotanica et Phytotaxonomica,* **14,** 145–166.

Olff, H. & Pegtel, D. M. (1994) Characterisation of the type and extent of nutrient limitation in grassland vegetation using a bioassay with intact sods. *Plant and Soil,* **163,** 217–224.

Oomes, M. J. M. & Van Der Werf, A. (1996) Restoration of species diversity in grasslands: The effect of grassland management and changes in ground water level. *Acta Botanica Gallica,* **143,** 451–461.

Patzelt, A. & Pfadenhauer, J. (1998) Keimungsbiologie und Etablierung von Niedermoor-Arten bei Ansaat duch Mähgutübertragung. *Zeitschrift für Ökologie und Naturschutz,* **7,** 1–13.

Pauli, D. (1998) *Plant species diversity and productivity in wetland communities: Patterns and processes,* PhD Thesis, Universität Zürich.

Peintinger, M. (1990) Fluctuations in population size of rare species in Molinion meadows in the area of Lake Constance (Germany). *Carolinea,* **48,** 69–84.

Sharpley, A., N. (1995) Soil phosphorus dynamics: agronomic and environmental impacts. *Ecological engeneering,* **5,** 261–279.

Shaver, G.R. (1983) Mineral nutrition and leaf longevity in *Ledum palustre:* the role of individual nutrients and the timing of leaf mortality. *Oecologia,* **56,** 160–165.

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

Tilman, D. (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs,* **57,** 189–214.

Tilman, D. (1996) Biodiversity: Population versus ecosystem stability. *Ecology,* **77,** 350–363.

Twolan Strutt, L. & Keddy, P. A. (1996) Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology,* **77,** 259–270.

Van Duren, I. C., Boeye, D. & Grootjans, A. P. (1997) Nutrient limitations in an extant and drained poor fen: implications for restoration. *Plant Ecology,* **133,** 91–100.

Verhoeven, J. T. A., Koerselman, W. & Meulman, A. F. M. (1996) Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management. *Trends in Ecology and Evolution,* **11,** 494–497.

Vermeer, J. G. (1986) The effect of nutrient addition and lowering of the water table on shoot biomass and species composition of a wet grassland community (*Cirsio-Molinietum*). *Acta Oecologica/ Oecologia Plantarum,* **7,** 145–155.

Wassen, M. J. & Joosten, J. H. J. (1996) In search of a hydrological explanation for vegetation changes along a fen gradient in the Biebrza Upper Basin (Poland). *Vegetatio,* **124,** 191–209.

Weiher, E., Wisheu, I. C., Keddy, P. A. & Moore, D. R. J. (1996) Establishment, persistence, and management implications of experimental wetland plant communities. *Wetlands,* **16,** 208–218.

Wetzel, P. R. & van der Valk, A. G. (1998) Effects of nutrient and soil moisture on competition between *Carex stricta, Phalaris arundinacea,* and *Typha latifolia. Plant Ecology,* **138,** 179–190.

Wirz-Kalender (1995) *Landwirtschaftliches Jahrbuch zum Wirz-Kalender.* 101. Jahrgang, Verlag Wirz, Aarau.

Zelesny, H. (1994) Vegetationskundliche und nährstoffökologische Untersuchungen im Übergangsbereich von Mehrschnitt-Wirtschaftsgrünland zu Streuwiese im Württembergischen Alpenvorland. *Dissertationes Botanicae,* **211,** 1–243.