

Zeitschrift: Bulletin of the Geobotanical Institute ETH
Herausgeber: Geobotanisches Institut, ETH Zürich, Stiftung Rübel
Band: 64 (1998)

Artikel: Research Note : the N:P ratio and the nutrient limitation of wetland plants
Autor: Güsewell, Sabine / Koerselmann, Willem / Verhoeven, Jos T.A.
DOI: <https://doi.org/10.5169/seals-377819>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 08.07.2025

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

RESEARCH NOTE

The N:P ratio and the nutrient limitation of wetland plants

SABINE GÜSEWELL*, WILLEM KOERSELMAN†
& JOS T.A. VERHOEVEN‡

**Geobotanisches Institut ETH Zürich, Gladbachstrasse 114, 8044 Zürich, Switzerland, †Kiwa N.V. Research and Consultancy, P.O. Box 1972, 3430 BB Nieuwegein, The Netherlands, and ‡Utrecht University, Department of Plant Ecology and Evolutionary Biology, P.O. Box 80084, 3584 CA Utrecht, The Netherlands; guesewell@geobot.umnw.ethz.ch*

Summary

1 Nutrient enrichment is one of the main factors threatening biodiversity in wetlands. Knowing which nutrient limits plant growth at a given site can help to predict the effects of nutrient enrichment, and to choose adequate measures to prevent or to mitigate these effects. The ratio of nitrogen to phosphorus concentration in aboveground plant biomass (N:P ratio) is an indicator whether biomass production of a given site is limited by nitrogen or phosphorus at the community level. We hypothesized that the same prediction might also be possible at the individual species level.

2 To investigate whether data from previous investigations qualitatively support our hypothesis we established a database with published data on (a) nutrient concentrations of wetland plant species, (b) site conditions, and (c) effects of fertilization. The database includes results from survey studies, and field and growth chamber experiments. A preliminary analysis of these data is presented in this contribution.

3 The N:P ratios measured in field surveys varied strongly among species within sites and among sites for a given species. Different study sites partly had distinct ranges of N:P ratios, whereas the ranges of N:P ratios of different plant species overlapped considerably. Data from fertilizing experiments in three Dutch fens suggest that species with high N:P ratio responded stronger to P fertilizer than species with low N:P ratio, with respect to both biomass and nutrient concentrations. Thus, the results appear to be consistent with our hypothesis.

4 Field and greenhouse experiments are currently carried out to test the main hypothesis more rigorously. Moreover, a detailed analysis of the database is planned once the latter has become more comprehensive. Readers which have data on nutrient concentrations of wetland plants are therefore kindly requested to provide their data for inclusion in the database.

Keywords: database, eutrophication, fens, fertilizing experiment, nature conservation, nutrient concentration

Bulletin of the Geobotanical Institute ETH (1998), 64, 77–90

Introduction

Nutrient enrichment of sites with natural or semi-natural vegetation is one of the main problems for nature conservation in central Europe (Klötzli 1986, 1987; Ellenberg 1989). Indeed, nutrient enrichment causes increased plant biomass production which often leads to lower species richness (e.g. Vermeer & Berendse 1983; Wheeler 1988). Moreover, many rare or endangered plant species can only subsist at low-productive sites (Ellenberg 1985; Dijk & Olf 1994). Maintaining or restoring low productivity is, therefore, one of the main targets of management in nature reserves. To reach this target most efficiently, measures should primarily focus on reducing the availability of the most limiting nutrient (Koerselman & Verhoeven 1995). A nutrient is called "limiting" if adding it increases the productivity of a plant or a site, whereas adding other nutrients has no effect. The limiting nutrient in wetlands is most frequently nitrogen (N) or phosphorus (P) (Koerselman & Verhoeven 1995; Wassen *et al.* 1995; Koerselman & Meuleman 1996; Boeye *et al.* 1997; Lammerts & Grootjans 1997), but limitation by potassium (K) also occurs, particularly on drained peat (van Duren *et al.* 1997). Biomass production can also be "co-limited" by two nutrients. One of them is then generally "primarily" limiting, i.e. more important than the other one (Koerselman & Meuleman 1996). Thus, management should aim to restrict the availability of either N, P or K, depending on the site. Since different measures are needed in each of these cases (Koerselman & Verhoeven 1995), knowing the most limiting nutrient can help to maintain valuable plant communities and rare wetland species.

A recent review of fertilization experiments (Koerselman & Meuleman 1996) has shown that the limiting nutrient in herbaceous

wetland communities can be determined based on the N and P concentrations in the aboveground plant biomass. In these experiments, biomass production was limited by phosphorus if the N concentration was more than 16 times the P concentration (N:P ratio >16), and by nitrogen if the N concentration was less than 14 times the P concentration (N:P ratio < 14). At intermediate values (N:P ratio between 14 and 16) either nitrogen, or phosphorus, or both nutrients could be limiting. This relationship is, however, only valid for sites that are not limited by potassium.

The relation established by Koerselman & Meuleman (1996) is based on results obtained at the vegetation level, i.e. on N:P ratios in the aboveground biomass (pooling all species) and on the response of the aboveground biomass to nutrient addition. For nature conservation, predicting effects of nutrient enrichment at the individual species level, i.e. changes in species composition, would be of particular interest. Increasing availability of a limiting nutrient generally increases the dominance of certain fast-growing species, whereas the less competitive species decrease or even disappear (e.g. Wheeler & Giller 1982; Egloff 1986; Aerts & Berendse 1988). Changes in species composition can also occur if a non-limiting nutrient is added to a site, even though total biomass does not increase (di Tommaso & Aarssen 1989; Verhoeven *et al.* 1996). Such changes cannot be predicted directly from the N:P ratio of the whole vegetation. This raises the question whether a prediction might be possible based on the N:P ratios of individual plant species (Shaver & Chapin III 1995; Wassen *et al.* 1995; Koerselman & Meuleman 1996; Lammerts & Grootjans 1997).

The relation between the N:P ratio of a given plant species at a given site and its response to fertilization is complex (Fig. 1).

Both of them can be assumed to depend on the relative amounts of N and P available to the species at that site. But how this relative nutrient availability is reflected in the N:P ratio of the species and its response to fertilization also depends on other factors which may differ among species and/or among sites.

Thus, Hayati & Proctor (1991) stated that “chemical analyses of plant material may be of only limited value as an indication of nutrient availability under natural conditions” because “there is substantial regulation in uptake” and because “variation in uptake often depends on interactions of diverse factors”.

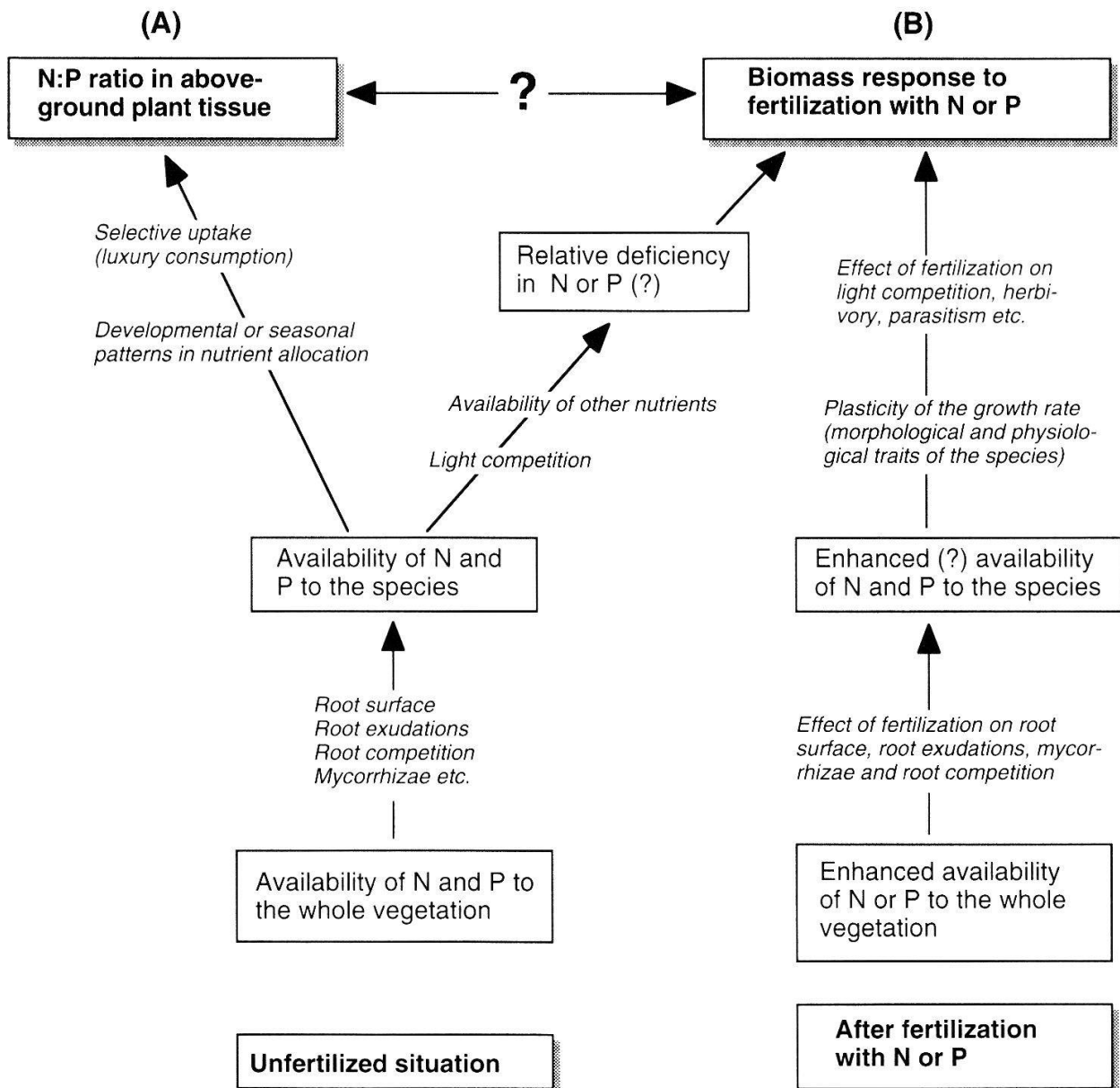


Fig. 1. Indirect and complex relation between (a) the N:P ratio of individual plant species and (b) the response of the biomass to fertilization with N or P. Both (a) and (b) depend on the availability of nutrients to the vegetation, which is increased if the site is fertilized. But various factors (*italic*) determine which fraction of these nutrients is available to the individual species, which fraction is taken up and allocated to the aboveground biomass, and whether increased availability of N or P results in higher biomass production. Interspecific and inter-site differences with respect to these factors might lead to different relations between N:P ratios and responses to fertilization.

Boller-Elmer (1977), Kaul (in Klötzli 1986, 1987), Kellermann & Zelesny (1993) and Brülisauer (1996) found rather inconsistent patterns in the variation of nutrient concentrations along gradients in productivity. However, all these authors considered the concentrations of N and P (and other nutrients) separately, not the N:P ratio.

Therefore, we are currently investigating how the N:P ratio of individual wetland species varies in response to differing N and P availability and how this ratio is related to the effects of fertilization with N or P. As a first step we established a database with data on nutrient concentrations published in previous studies. In this research note we describe the structure of the database and some patterns emerging from the data. We discuss whether they qualitatively support our hypothesis that the N:P ratio of individual species can be used to predict their response to nutrient enrichment. We also present the experiments planned to test this hypothesis more rigorously, and end with a call for more data which might be included in the database.

The database

Many studies have already investigated the nitrogen and phosphorus concentrations of wetland plants, including field surveys, field experiments (e.g. Verhoeven & Schmitz 1991) and more controlled growth experiments (garden, greenhouse or growth chamber, e.g. McJannet *et al.* 1995; Perez Corona *et al.* 1996). In most field studies, only the aboveground biomass was harvested, and it was analysed as a whole; some studies also analysed the belowground biomass (e.g. Pfadenhauer & Lütke-Twenhöven 1986; Marti 1994) or individual plant parts (e.g. Hocking 1989b; Thompson *et al.* 1997). In controlled growth experiments the whole

plants were generally analysed. The questions addressed varied widely. They were mostly related to nutrient availability and nutrient limitation (e.g. Buttler 1987; Hayati & Proctor 1991; Verhoeven & Schmitz 1991; Koerselman & Meuleman 1994; Zelesny 1994; Shaver & Chapin III 1995; Wassen *et al.* 1995), to nutrient allocation and nutrient cycling (e.g. Ganzert & Pfadenhauer 1986, Pfadenhauer & Lütke-Twenhöven 1986; Hocking 1989a,b), to relations between nutrient concentrations and morphological, physiological or functional attributes (e.g. McJannet *et al.* 1995; Thompson *et al.* 1997), or to the effects of management (e.g. Warnke-Grüttner 1990). Accordingly, some studies measured other important variables, such as the concentration of various nutrients, the chemical composition of soil or soil water, peak biomass or biomass production, morphological traits, or the effects of fertilization. The aim of our database is to assemble all these data, both in order to analyse them and to make them available to other researchers on the world wide web.

The structure of the database is presented in Fig. 2. Data are included in five separate files. One file contains species data. Three files contain information on sites and/or experimental conditions for (a) survey studies, (b) field experiments, and (c) garden, greenhouse or growth chamber experiments, respectively. Data in these files are related to the species data through linking fields identifying the site and/or the treatment. Finally, a "reference" file contains a standard literature database and is linked to the other files through the "reference" field. Thus, of the five files building up the database, two are common to all types of studies and three are specific to each type. A particular data set always consists of data contained in three of the five files. This relational structure was chosen to reduce

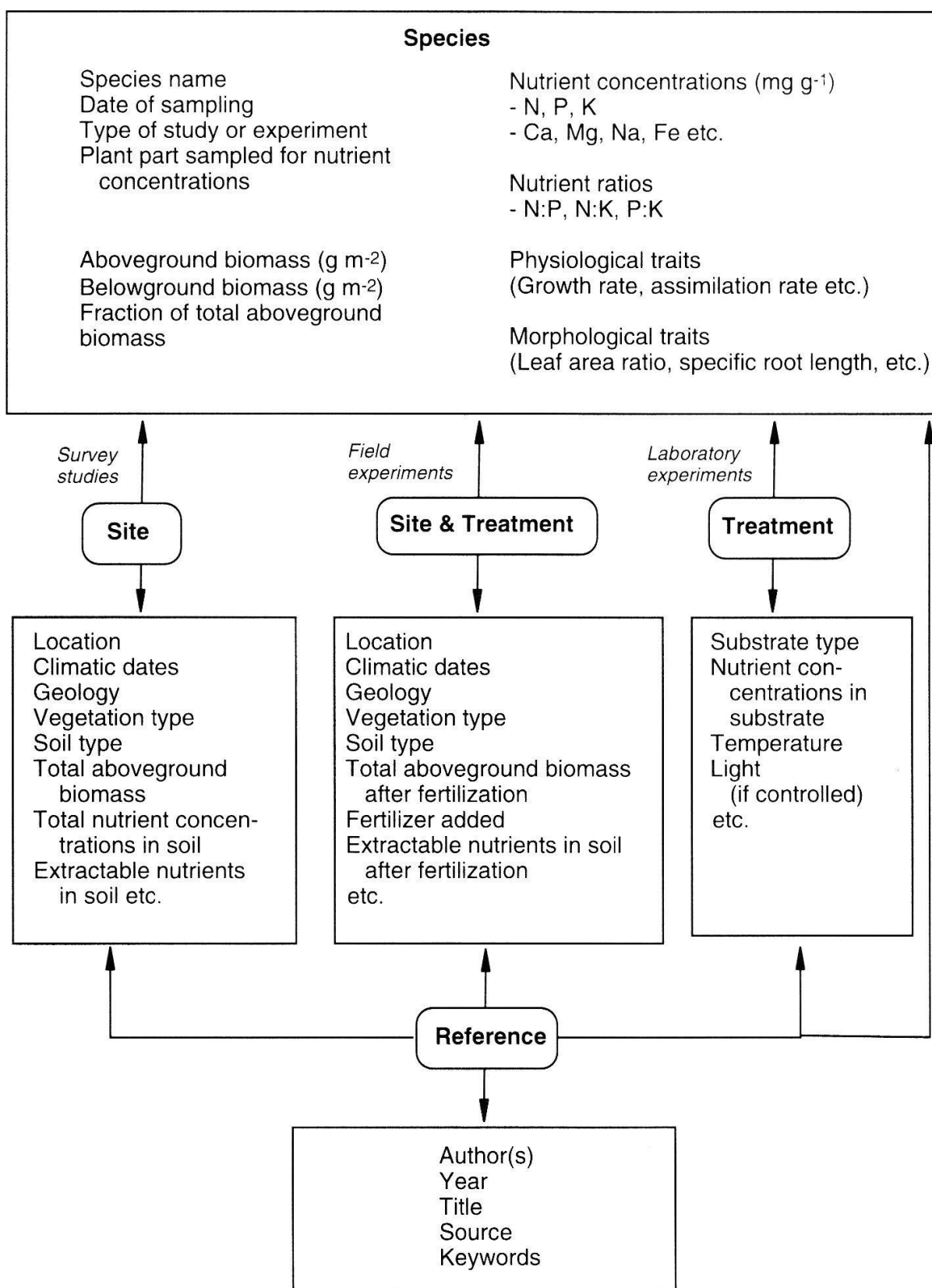


Fig. 2. Relational structure of the nutrient concentrations database. Nutrient and biomass data of individual wetlands plant species are contained in the "species" file. Information on growth conditions is stored in three separate files. Each of these files is particular to one type of study and linked to the "species" file by the "site", "site/treatment" or "treatment" field, respectively. The source of the data is indicated in the "reference" file.

the number of empty fields, to avoid redundancy within the database, and to facilitate the separate analysis of data from surveys, field experiments and more controlled experiments.

The database currently contains data from most of the above publications (those from Hocking 1989a,b; McJannet *et al.* 1995; Shaver & Chapin III 1995; and Wassen *et al.* 1995 could not be incorporated yet). Some publications give only mean values for several sites (Buttler 1987; Marti 1994; Thompson *et al.* 1997); on our request authors kindly provided the original data.

Data analysis

Only values of N:P ratios in the aboveground biomass measured in the field during the summer (June–September) were considered in the preliminary analysis of the database. The variation among and within sites was investigated using all sites in which at least five species had been sampled; the variation among and within species was investigated with the species that had been sampled at five or more sites. Thompson *et al.* (1997) had determined the nutrient concentrations in leaves only; therefore, their data were analysed separately.

The effect of fertilization was investigated using unpublished data from the experiment of Verhoeven & Schmitz (1991). This experiment had been carried out in three fens where small plots were fertilized with N, P, K or NPK; control plots were unfertilized. Aboveground biomass was measured at the vegetation level, but nutrient concentrations were determined separately for each of the species. The effect of fertilization on nutrient concentrations and on the N:P ratio was calculated as the difference between fertilized and control plots, using log-transformed data, so that

relative differences were considered. Since potassium fertilization had no effect on biomass or nutrient concentrations at any of the sites (Verhoeven & Schmitz 1991), differences between NPK-fertilized and N-fertilized plots, as well as differences between NPK-fertilized and P-fertilized plots were also included in the analysis as the effects of phosphorus and nitrogen fertilization, respectively.

Preliminary results and further research

VARIATION IN THE N:P RATIO

The N:P ratio of individual plant species varied considerably both among and within sites (Fig. 3a), and likewise, both among and within species (Fig. 3b,c). Some sites had distinct ranges of N:P ratios, and the variability among sites was greater than within sites (Table 1) but no systematic difference appeared between rich fens, poor fens and dune slacks. The ranges of N:P ratios of most species overlapped considerably, particularly when based on nutrient concentrations in leaves, and the variability among and within species was similar. In general, dicots tended to have lower N:P ratios than monocots in total aboveground biomass, but not in the leaves. The within-site variation in N:P ratio was similar for all sites, and the within-species variation was fairly similar for most species. The N:P ratios were, in general, more variable than the N concentrations, but less variable than P concentrations. However, N:P ratios appeared to be relatively more variable than both N and P concentrations when differences among sites were considered.

The within-site variation in the N:P ratios of individual species might be an indication that the same site can be experienced as P-poor for some species and as P-rich for others (Koerselman & Verhoeven 1995), maybe due to specific uptake mechanisms depending on

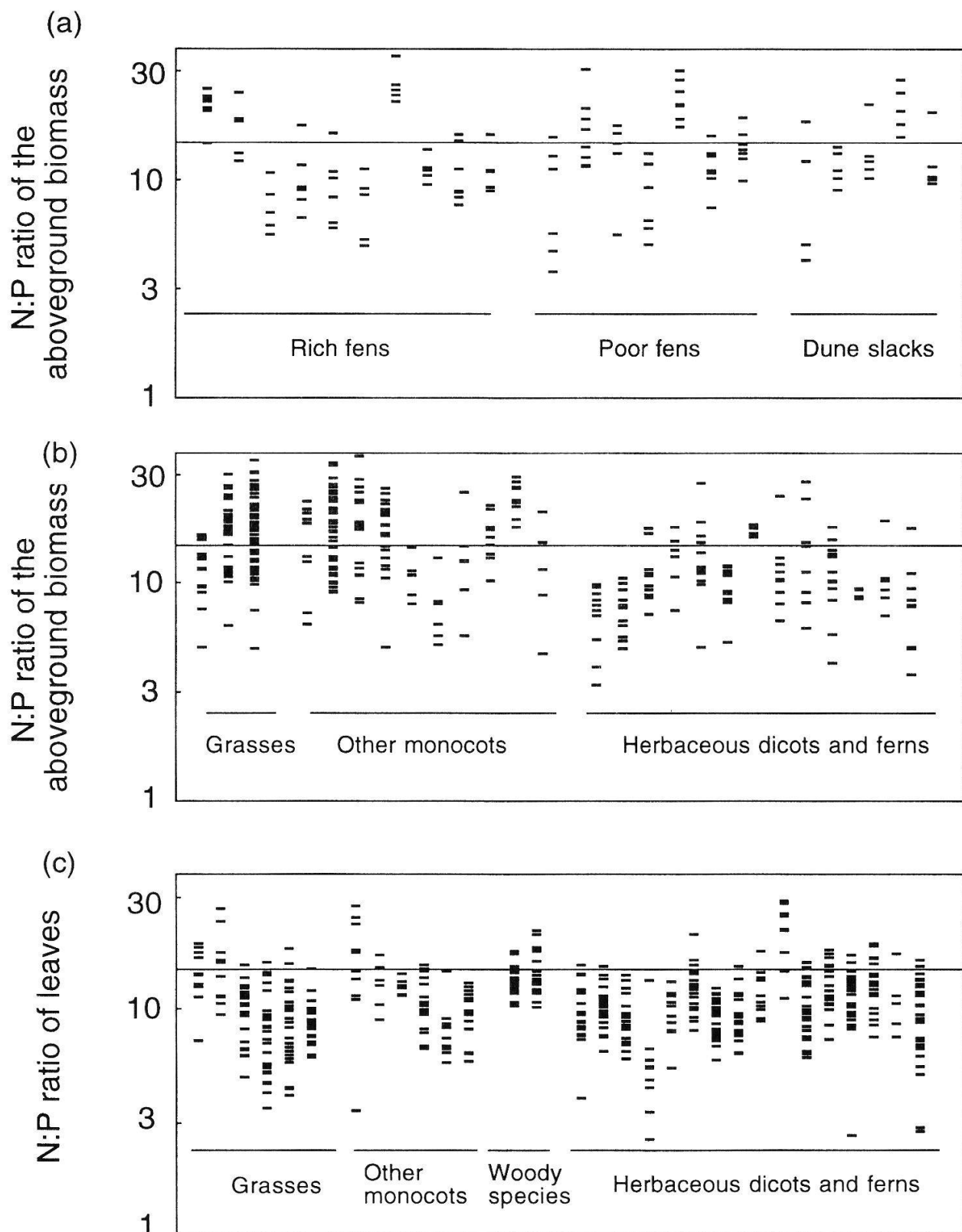


Fig. 3. Variability of N:P ratios (a) among species growing together at the same site, and (b, c) among sites for the same species. Each column along the x-axis represents one site in (a) and one species in (b) and (c), whereas the individual symbols represent different species in (a) and different sites in (b) and (c). Horizontal lines indicate a N:P ratio of 15. See text for the source of data for (a) and (b). Data in (a) and (b) are from various authors, data in (c) from Thompson et al. (1997).

Table 1. Variability of the N- and P-concentration and the N:P ratio in the aboveground biomass of individual plant species. Variability "among", is the coefficient of variation of mean N:P ratios per species or per site; and variability "within" the mean of the coefficients of variation calculated separately for each species or site

	Coefficient of variation (%)		
	N _{conc}	P _{conc}	N:P ratio
Among species	26.3	39.3	32.5
Within species	26.9	37.0	32.7
Among sites	29.3	38.7	40.6
Within sites	26.0	33.4	31.3

mycorrhizal infection or root exudations (Perez Corona *et al.* 1996; Schachtman *et al.* 1998). Whether the slight difference in N:P ratio between monocots and dicots (Fig. 3b) actually indicates some difference in nutrient limitation still needs to be investigated. Monocots (graminoids) and dicots were often found to differ in their responses to fertilizer treatments, but no consistent overall pattern could be established (di Tommaso & Aarssen 1989).

The data, particularly those for leaf nutrient concentrations (Fig. 3c) suggest that differences in N:P ratio reflect both differences in growth conditions (e.g. in nutrient availability) and inherent physiological characteristics of the species although the latter are only of minor importance. McJannet *et al.* (1995) found strong interspecific variation in the N:P ratio of 41 wetland species grown under identical conditions. In their study, however, plants were grown at high light and nutrient supply. It seems plausible that physiological traits of the species determine their pattern of nutrient uptake under optimal conditions, whereas the relative availability of nutrients is decisive when the latter are in short supply.

The main problem with the data presented in Fig. 3 is that interspecific differences are

confounded with differences among sites because the several species were not sampled at the same number and type of sites. Seasonal changes have probably also affected the results. The N:P ratio is likely to change little in early summer because it is not affected by the "dilution" of nutrients in growing aboveground biomass, but substantial change may occur in late summer because of differences between N and P in the time and extent of translocation to belowground parts (e.g. Pfadenhauer & Lütke-Twenhöven 1986; Hocking 1989a; Warnke-Grüttner 1990). Due to our rather broad range of sampling dates (June–September) we may have overestimated the variation among and within species as well as the variation among sites. Therefore, the relative contribution of interspecific variation and growth conditions to variation in the N:P ratio cannot be determined exactly based on these data. To determine the relative importance of these two factors we are currently growing cuttings of various wetland species under differing conditions and will measure their nutrient concentrations at the end of the summer. In a first experiment we vary the N:P ratios of nutrient solutions (five ratios: 1.67, 5, 15, 45, 135) as well as the general nutrient level (simple, threefold and nine fold) and light supply (c. 10% and 90% shade). Further experiments are planned to investigate whether the type of substrate and the water level also affect the N:P ratio and whether such effects – if significant – differ among species.

N:P RATIO AND NUTRIENT AVAILABILITY

In the experiment of Verhoeven & Schmitz (1991) the nutrient concentrations of individual plant species were determined in plots fertilized with either N, P, K or NPK, as well as in unfertilized plots. The N:P ratios were on average 28% higher in N-fertilized plots

Table 2. Mean N:P ratio in the aboveground biomass of individual plant species harvested on 16 July 1987 in experimental plots with differing fertilizer treatment (\pm SD, if species were present in more than one of the five replicates). Site abbreviations are Ho, Het Hol; Mo, Molenpolder; We, Westbroek polder. Unpublished data from the experiment of Verhoeven & Schmitz (1991)

Species	Site	N:P ratio in the aboveground biomass				
		Control	N	P	K	NPK
<i>Calamagrostis canescens</i>	Mo	12.7	29.9	3.7	13.9	6.9 \pm 0.5
<i>Carex canescens</i>	We	19.4			21.2	8.4
<i>Carex diandra</i>	We	14.5	19.1 \pm 6.8	5.5	7.2	
	Mo		22.9	6.2	10.4	
<i>Carex lasiocarpa</i>	Ho	17.6	32.2	9.7 \pm 0.3	17.5 \pm 1.6	9.7
<i>Carex paniculata</i>	Mo	10.7 \pm 1.9	28.1			7.2
<i>Carex rostrata</i>	We	13.2 \pm 0.5	13.9 \pm 1.1	8.2 \pm 0.8	12.5 \pm 1.8	7.9 \pm 0.5
<i>Equisetum fluviatile</i>	We	9.9 \pm 0.7	12.1 \pm 1.6	8.3 \pm 0.4	10.1 \pm 0.2	8.7 \pm 0.5
<i>Equisetum palustre</i>	We	16.2 \pm 0.8	10.6	8.2	10.4 \pm 0.3	9.4
<i>Erica tetralix</i>	Ho	25.5	26.5 \pm 11.0	2.8	26.7 \pm 1.6	8.1 \pm 0.6
<i>Juncus subnodulosus</i>	Ho	22.0 \pm 0.5	27.1	8.9	22.0 \pm 0.7	13.9
	Mo	10.1 \pm 3.2	14.0 \pm 2.8	5.2 \pm 1.1	10.1 \pm 2.1	5.9 \pm 3.4
<i>Molinia caerulea</i>	Ho	31.7 \pm 4.8	45.0 \pm 8.9	6.8 \pm 2.1	26.1 \pm 9.9	8.9 \pm 1.0
<i>Myrica gale</i>	Ho	28.7 \pm 4.1	32.4 \pm 7.2	12.3 \pm 2.7	31.6 \pm 1.6	14.9 \pm 1.5
<i>Phragmites australis</i>	Ho	19.2	18.6 \pm 6.0	13.0 \pm 0.6	18.6 \pm 1.8	14.8 \pm 4.8
	Mo	7.4 \pm 0.6	10.3 \pm 1.7	7.4 \pm 1.7	7.8 \pm 0.6	8.2 \pm 0.2
<i>Potentilla palustris</i>	We	12.5 \pm 0.7	11.4 \pm 3.3	5.3 \pm 0.8	16.1	7.4 \pm 0.8
<i>Sphagnum</i> spp.	Ho	22.0 \pm 5.6	14.9 \pm 6.8	4.4 \pm 0.8	27.8 \pm 1.2	10.4
	Mo	15.9 \pm 2.3	23.5 \pm 2.1	3.7 \pm 0.6	14.9 \pm 5.2	5.8 \pm 0.2
	We	13.8 \pm 0.9	15.2 \pm 1.6	4.3 \pm 0.1	12.5 \pm 3.1	7.2 \pm 1.3
<i>Thelypteris palustris</i>	Mo	11.0 \pm 2.8	24.8 \pm 6.5	6.8 \pm 0.2	12.0 \pm 3.2	9.3

than in the controls, 39% higher in NPK-fertilized than in P-fertilized plots, 60% lower in P-fertilized plots than in controls, and 55% lower in NPK-fertilized plots than in the N-fertilized plots (Table 2). Thus, the differences in nutrient availability were reflected in strong changes in the N:P ratio already in the same growing season.

The effect of fertilizer on the N:P ratio, as measured by these relative differences, strongly differed among species at each of the study sites and was correlated with the initial N:P ratio (Fig. 4). The lower the N:P ratio of a species in control plots or in P-fertilized plots the more this N:P ratio increased under nitrogen fertilization ($r = -0.42$). The relation was similar for the three sites in spite of their dif-

ferent nutrient limitation at the vegetation level (Fig. 4a). Likewise, the higher the N:P ratio of a species in control plots or in N-fertilized plots, the more the ratio decreased due to phosphorus fertilization ($r = -0.67$, Fig. 4b). These correlations suggest that the different initial N:P ratios reflected differences in relative nutrient availability and demand of the various species, rather than intrinsic differences in chemical composition.

Because of their practical significance, relations between nutrient availability, nutrient uptake by plants and nutrient concentrations in biomass have been extensively studied in agricultural research. Considerable differences were found not only among species, but also among varieties (cultivars) (e.g.

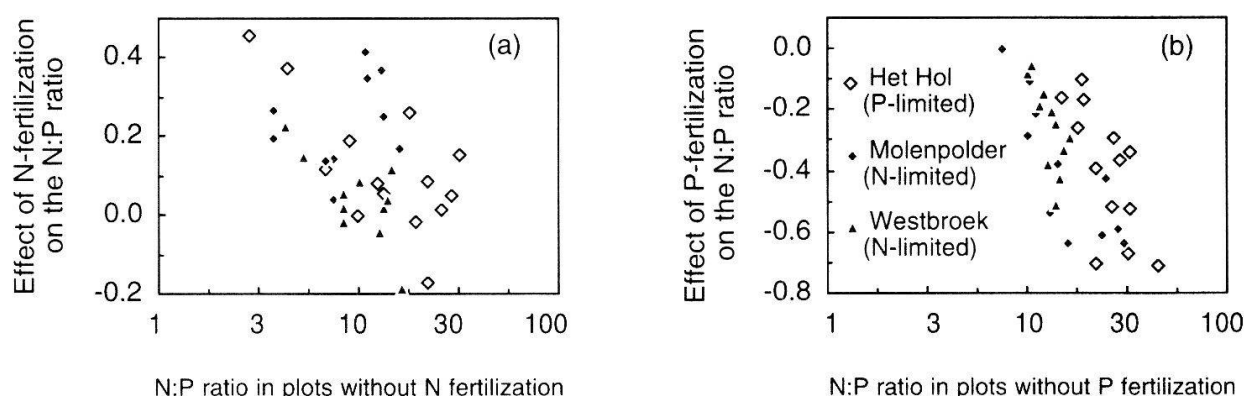


Fig. 4. Relation between the N:P ratio in unfertilized plots and the effect of (a) nitrogen fertilization, and (b) phosphorus fertilization on the N:P ratio of wetland plants. Effects of fertilizer were measured as differences between logarithms of N:P ratios in fertilized and in corresponding unfertilized plots. Unpublished data from an experiment of Verhoeven & Schmitz (1991).

Gahoonia & Nielsen 1996; Horst *et al.* 1996). Spatial and temporal patterns of rooting as well as differences in nutrient allocation and translocation are important (Horst *et al.* 1996; van Vuuren *et al.* 1996; Wendt *et al.* 1996). Moreover, the relations were influenced by various other factors, such as soil type and temperature (Hoffmann & Jungk 1996), water conditions (Heckathorn 1997), or interactions with other nutrients (Schjørring 1986; Hartikainen & Yli-Halla 1996). A relation between the N:P ratio of plant species and their nutrient limitation seems, therefore, more likely to be found for a specific site and specific experimental conditions than for a broad range of sites with much variation in these other factors.

Experimental work in growth chambers has shown that nutrient ratios of seedlings exactly correspond to the ratio at which nutrients are supplied, providing supply increases exponentially at a constant rate which is lower than the maximal relative growth rate of the seedlings (Ingestad 1979; Ingestad & Lund 1979). There are various reasons why such a correspondence cannot be expected for field experiments: (1) Nutrient supply is not exponential in the field. (2) Ingestad (1979) ana-

lysed whole plants, whereas only the aboveground biomass can normally be sampled and analysed in field experiments. Investigations in monodominant stands revealed that N:P ratios vary considerably between aboveground and belowground biomass (Pfadenhauer & Lütke-Twenhöven 1986; Marti 1994). (3) Nutrient storage in belowground parts may modify the relation between N and P availability and the N:P ratio of individual species. For example, *Phragmites australis* was found to store around 80% of the phosphorus standing stock, but only around 60% of the nitrogen standing stock in its rhizomes (Granéli 1990). This means that the N:P ratio of nutrient uptake must be higher than the N:P ratio in the aboveground plant biomass. It seems likely that in such a situation the N:P ratio of the biomass reflects the nutrient shortage experienced by the plant more accurately than the N:P ratio of nutrient supply by the site or of nutrient uptake by the plant.

In our growth experiment we will investigate how the N:P ratio in plants varies in response to different N:P ratios in the nutrient solution. Moreover, the manipulation of other factors (light, productivity, soil type, water

level, competitors) will indicate whether and how these factors affect the relation between nutrient availability and N:P ratio. If these relations and effects differ among species, they will be related to the morphological or physiological attributes of the species.

NUTRIENT AVAILABILITY AND RESPONSE TO FERTILIZATION

In their fertilizing experiment Verhoeven & Schmitz (1991) did not determine the biomass of the individual species, so that the relation between N:P ratio and the effect of nutrient enrichment on the biomass could not be investigated directly. In order to estimate the effect of nitrogen fertilization indirectly, we used the fact that at the community level, nitrogen fertilization partly increased the above-ground biomass, but not the total uptake of phosphorus (Verhoeven & Schmitz 1991). This suggests that the vegetation took up most of the available phosphorus both in unfertilized and in nitrogen-fertilized plots ("luxury uptake"). Higher biomass due to nitrogen fertilization would, therefore, be reflected by lower phosphorus concentration.

Assuming that this was also true for individual species, we tested whether the effect of nitrogen fertilization on phosphorus concentration (i.e. presumably, on biomass) depended on the N:P ratio in unfertilized plots. There was, indeed, a certain correlation ($r = 0.39$, $P < 0.1$). If our assumption is true, this correlation would indicate that the biomass of species with low N:P ratio increased more strongly after nitrogen fertilization than the biomass of species with high N:P ratio, as we hypothesized.

No correlation was not found between the N:P ratio and the effect of phosphorus fertilization on nitrogen concentration ($r = 0.29$, $P > 0.1$). A possible explanation is that there was no luxury uptake of nitrogen in the

unfertilized plots. This was suggested by the fact that phosphorus fertilization increased nitrogen uptake at the same time as biomass at the community level (Verhoeven & Schmitz 1991). The consequence would be that phosphorus fertilization could increase the biomass of a species without decreasing its nitrogen concentration.

The assumptions on which we based our interpretation of the data are hypothetical and so far not confirmed by experiments (e.g. Vermeer 1986). Therefore, the relation between the N:P ratio and the effect of nutrient enrichment needs more rigorous testing through direct investigation. We plan to do this in the field using similar methods as Verhoeven & Schmitz (1991), but including measures of the biomass of individual species. Additionally, we will carry out glass-house experiments in which plants are grown at differing N:P ratios from March to June, before being randomly assigned to one of four fertilizer treatments (low N low P, low N high P, high N low P, high N high P) for three months. Thus, it can be examined whether the biomass response of plants to these treatments is related to their initial N:P ratios, and whether effects differ among species. If relations are found to be significant, relatively independent of other factors (e.g. light conditions, soil type), and similar across species, and if they are further confirmed by field experiments, we may assume that the N:P ratio is a useful tool to predict short-term effects of nutrient enrichment, not only at the vegetation level (Koerselman & Meuleman 1996) but also at the level of individual species.

Call for data to add to the database

As already mentioned above, our preliminary interpretation of the data from the literature is still speculative because several factors were

not taken into account. Much more attention needs to be paid to the seasonal variation of the N:P ratio, to its variation among plant parts, and to its dependence on other site factors. The variability of the N:P ratio should also be compared to the variability of other ratios, particularly the N:K and P:K ratios. We would then like to examine how these various ratios are related to the relative abundance of the species, to site productivity, and to nutrient concentrations in the soil. The data itself will be made available on the world wide web for use by other researchers. For all this it would be important that the database becomes as comprehensive as possible. *We therefore kindly request all readers who have unpublished data on nutrient concentrations of wetland plants to send them to the first author, in electronic or in paper form, to become included into the database.*

Acknowledgements

We sincerely thank authors who kindly accepted to provide their data for inclusion in the database, as well as F. Klötzli, B. Köhler, J. Kollmann and two anonymous referees for commenting on an earlier draft of the manuscript. T. Fotsch, A. Hegi and S. Locher helped to establish the first of the experiments mentioned above. This experiment is financed by the Swiss Federal Office of Environment, Forest and Landscape (BUWAL); the other experiments will be financed by grant ENV4-CT97-5075 from the Commission of the European Communities.

References

- Aerts, R. & Berendse, F. (1988) The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio*, **76**, 63–69.
- 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.
- Boller-Elmer, K. (1977) Stickstoff-Düngungseinflüsse von Intensiv-Grünland auf Streu- und Moorwiesen. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **63**, 1–103.
- Brülisauer, A. (1996) *Zu den Ursachen der Verschilfung von Streuwiesen im Schweizer Mittelland*. Forschungsbericht BUWAL, Zürich.
- Buttler, A. (1987) *Etude écosystématique des marais non boisés de la rive Sud du lac de Neuchâtel (Suisse)*. Institut de botanique, Neuchâtel.
- di Tommaso, A. & Aarssen, L.W. (1989) Resource manipulations in natural vegetation: a review. *Vegetatio*, **84**, 9–29.
- Dijk, E. & Olff, H. (1994) Effects of nitrogen, phosphorus and potassium fertilization on field performance of *Dactylorhiza majalis*. *Acta Botanica Neerlandica*, **43**, 383–392.
- Egloff, T. (1986) Auswirkungen und Beseitigung von Düngungseinflüssen auf Streuwiesen. Eutrophierungssimulation und Regenerationsexperimente im nördlichen Schweizer Mittelland. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **89**, 1–183.
- Ellenberg, H. jun. (1985) Veränderungen der Flora Mitteleuropas unter dem Einfluss von Düngung und Immissionen. *Schweizerische Zeitschrift Forstwesen*, **136**, 19–39.
- Ellenberg, H. jun. (1989) Eutrophierung – das gravierendste Problem im Naturschutz. *NNA-Berichte*, **2**, 27–30.
- Gahoonia, T.S. & Nielsen N.E. (1996) Variation in acquisition of soil phosphorus among wheat and barley genotypes. *Plant and Soil*, **178**, 223–230.
- Ganzert, C. & Pfadenhauer, J. (1986) Seasonal dynamics of shoot nutrients in *Schoenus ferrugineus* (Cyperaceae). *Holarctic Ecology*, **9**, 137–142.
- Granéli, W. (1990) Standing crop and mineral content of reed in Sweden – management of reed stands to maximize harvestable biomass. *Folia Geobotanica et Phytotaxonomica*, **25**, 291–302.
- Hartikainen, H. & Yli-Halla, M. (1996) Solubility of soil phosphorus as influenced by urea. *Zeitschrift für Pflanzenernährung und Bodenkunde*, **159**, 327–332.
- Hayati, A.A. & Proctor, M.C.F. (1991) Limiting nutrients in acid-mire vegetation: peat and plant analysis and experiments in plant responses to added nutrients. *Journal of Ecology*, **79**, 75–95.

- Heckathorn, S.A., DeLucia, E.H. & Zielinski, R.E. (1997) Contribution of drought-related decreases in foliar nitrogen concentration to decreases in photosynthetic capacity during and after drought in prairie grasses. *Physiologia Plantarum*, **101**, 173–182.
- Hocking, P.J. (1989a) Seasonal dynamics of production, and nutrient accumulation and cycling by *Phragmites australis* (Cav.) Trin. ex Stuedel in a nutrient-enriched swamp in inland Australia. I. Whole plants. *Australian Journal of Marine and Freshwater Research*, **40**, 421–444.
- Hocking, P.J. (1989b) Seasonal dynamics of production, and nutrient accumulation and cycling by *Phragmites australis* (Cav.) Trin. ex Stuedel in a nutrient-enriched swamp in inland Australia. II. Individual Shoots. *Australian Journal of Marine and Freshwater Research*, **40**, 445–464.
- Hoffmann, C. & Jungk, A. (1996) Influence of soil temperature and soil compaction on growth and P uptake of sugar beet. *Zeitschrift für Pflanzenernährung und Bodenkunde*, **159**, 263–270.
- Horst, W.J., Abdou, M. & Wiesler, F. (1996) Differences between wheat cultivars in acquisition and utilization of phosphorus. *Zeitschrift für Pflanzenernährung und Bodenkunde*, **159**, 155–161.
- Ingestad, T. (1979) Nitrogen stress in birch seedlings. II. N, K, P, Ca, and Mg nutrition. *Physiologia Plantarum*, **45**, 148–157.
- Ingestad, T. & Lund, A.-B. (1979) Nitrogen stress in birch seedlings. I. Growth technique and growth. *Physiologia Plantarum*, **45**, 148–157.
- Kellermann, S. & Zelesny, H. (1993) Möglichkeiten der Anwendung von Nährstoffgehalten einzelner Arten zur Standortscharakterisierung. *Bericht des Instituts für Landschafts- und Pflanzenökologie, Universität Hohenheim, Stuttgart*, **2**, 231–242.
- Klötzli, F. (1986) Tendenzen zur Eutrophierung in Feuchtgebieten. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **87**, 343–361.
- Klötzli, F. (1987) Régions humides oligotrophes dans notre paysage eutrophe. Augmentation de l'expulsion anthropogène de matières nutritives (N, P). *Giornale Botanico Italiano*, **121**, 101–120.
- Koerselman, W. & Meuleman, A.F.M. (1994) *Groeibeperkende voedingsstoffen in verschillende typen duinvalleien; resultaten van bemestingsexperimenten*. Kiwa N.V. Research and Consultancy, Nieuwegein (NL).
- 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.
- Koerselman, W. & Verhoeven, J.T.A. (1995) Eutrophication of fen ecosystems: external and internal nutrient sources and restoration strategies. *Restoration of Temperate Wetlands* (eds. B.D. Wheeler, S.C. Shaw, W.J. Fojt & R.R. Allan), 91–112. John Wiley & Sons, Chichester.
- Lammerts, E.J. & Grootjans, A.P. (1997) Nutrient deficiency in dune slack pioneer vegetation: a review. *Journal of Coastal Conservation*, **3**, 87–94.
- Marti, K. (1994) Zum Standort von *Magnocaricion*-Gesellschaften in der Schweiz. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **120**, 1–97.
- McJannet, C.L., Keddy, P.A. & Pick, F.R. (1995) Nitrogen and phosphorus tissue concentrations in 41 wetland plants: A comparison across habitats and functional groups. *Functional Ecology*, **9**, 231–238.
- Perez Corona, M.E., van der Klundert, J. & Verhoeven, J.T.A. (1996) Availability of organic and inorganic phosphorus compounds as phosphorus sources for *Carex* species. *New Phytologist*, **133**, 225–231.
- Pfadenhauer, J. & Lütke-Twenhöven, F. (1986) Nährstoffökologie von *Molinia coerulea* und *Carex acutiformis* auf baumfreien Niedermoores des Alpenvorlandes. *Flora*, **178**, 257–166.
- Schachtman, D.P., Reid, R.J. & Ayling, S.M. (1998) Phosphorus uptake by plants: from soil to cell. *Plant Physiology*, **116**, 447–453.
- Schjørring, J.K. (1986) Nitrate and ammonium absorption by plants growing at a sufficient or insufficient level of phosphorus in nutrient solutions. *Plant and Soil*, **91**, 313–318.
- Shaver, G.R. & Chapin III, F.S. (1995) Long-term responses to factorial NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography*, **18**, 259–275.
- Thompson, K., Parkinson, J.A., Band, S.R. & Spencer, R.E. (1997) A comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytologist*, **136**, 679–689.
- van Duren, I.C., Boeye, D. & Grootjans, A.P. (1997) Nutrient limitations in an extant and degraded poor fen: implications for restoration. *Plant Ecology*, **133**, 91–100.

- van Vuuren, M.M.I., Robinson, D. & Griffiths, B.S. (1996) Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. *Plant and Soil*, **178**, 185–192.
- Verhoeven, J.T.A., Beltman, B. & De Caluwe, H. (1996) Changes in plant biomass in fens in the Vechtplassen area, as related to nutrient enrichment. *Netherlands Journal of Aquatic Ecology*, **30**, 227–237.
- Verhoeven, J.T.A. & Schmitz, M.B. (1991) Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochemistry*, **12**, 135–148.
- Vermeer, J.G. (1986) The effect of nutrients on shoot biomass and species composition of wetland and hayfield communities. *Acta Oecologica*, **7**, 31–41.
- Vermeer, J.G. & Berendse, F. (1983) The relationship between nutrient availability, shoot biomass and species richness composition in grassland and wetland communities. *Vegetatio*, **53**, 121–126.
- Warnke-Grüttner, R. (1990) Ökologische Untersuchungen zum Nährstoff- und Wasserhaushalt in Niedermooren des westlichen Bodenseegebiets. *Dissertationes Botanicae*, **148**, 1–214.
- Wassen, M.J., Olde Venterink, H.G.M. & De Swart, E.O.A.M. (1995) Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *Journal of Vegetation Science*, **6**, 5–16.
- Wendt, J., Jungk, A. & Claassen, N. (1996) Höhe der Erhaltungsdüngung und Ausnutzung von Düngerphosphat vor dem Hintergrund der P-Alterung im Boden. *Zeitschrift für Pflanzenernährung und Bodenkunde*, **159**, 271–278.
- Wheeler, B.D. (1988) Species richness, species rarity and conservation evaluation of rich-fen vegetation in Lowland England and Wales. *Journal of Applied Ecology*, **25**, 331–353.
- Wheeler, B.D. & Giller, K.E. (1982) Species richness of herbaceous fen vegetation in Broadland, Norfolk, in relation to the quantity of above-ground material. *Journal of Ecology*, **70**, 179–200.
- Zelesny, H. (1994) Vegetationskundliche und nährstoffökologische Untersuchungen im Übergangsbereich von Mehrschnitt-Wirtschaftsgrünland zu Streuwiese im Württembergischen Alpenvorland. *Dissertationes Botanicae*, **211**, 1–243.

Received 23 April 1998

revised version accepted 18 June 1998