The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation

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Summary

1. Nutrient limitation (mostly N or P) is a driving force in ecosystem development. Current techniques to determine the nature of nutrient limitation use laborious fertilization experiments.

2. It was hypothesized that the N:P ratio of the vegetation directly indicates the nature of nutrient limitation on a community level (N vs. P limitation). This hypothesis was tested by reviewing data on fertilization studies in a variety of European freshwater wetland ecosystems (bogs, fens, wet heathlands, dune slacks, wet grasslands). In a subset of the data (dune slacks) between-site intraspecific variation and within-site interspecific variation in nutrient content and N:P ratio was studied in five plant species.

3. A review of 40 fertilization studies reveals that an N:P ratio > 16 indicates P limitation on a community level, while an N:P ratio < 14 is indicative of N limitation. At N:P ratios between 14 and 16, either N or P can be limiting or plant growth is co-limited by N and P together. In only one out of 40 fertilization studies, the N:P ratio gave a false indication of the nature of nutrient limitation. Measuring the N:P ratio of the vegetation is a simple and cheap alternative to fertilization studies. The method can only be used under conditions where either N or P controls plant growth.

4. The dataset contains a large variety of vegetation types and plant species, and 11 of the 40 sites were near-mono cultures. This suggests that interspecific differences in critical N:P ratios among species may be insignificant. However, a rigorous test of this hypothesis is required.

5. A survey in 18 dune slacks showed large within-site variation in N:P ratio among five species (Calamagrostis epigejos, Phragmites australis, Lycopus europaeus, Mentha aquatica and Eupatorium cannabinum). The N:P ratios of the five species suggested that within plant communities species can be differentially limited by N or P. Moreover, species with an N:P ratio that suggested P-limitation were found at sites where N controlled community biomass production, and vice versa. Between-site intraspecific variation in N and P contents and N:P ratios was also large, and about equal for the five species. This illustrates the plasticity of plant species with respect to N and P contents, probably in response to differences in N and P supply ratios.

6. The vegetation N:P ratio is of diagnostic value and its use may increase our understanding of numerous facets of physiological, population, community and ecosystem ecology.

Key-words: fertilization, nutrient availability, tissue N, tissue P, wetland.


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Introduction

Resource availability is a driving force in ecosystem succession and nutrients are among the most important plant resources that structure plant communities (Tilman 1985; Vitousek & Walker 1987; DiTomasso & Aarsen 1989; Grace & Tilman 1990; Vitousek & Howarth 1991). Nutrient limitation strongly affects competition between plant species, as species vary in their ability to cope with low nutrient resources. There is an evolutionary trade-off between plant features advantageous under nutrient-poor conditions and fea-
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Features that serve as adaptations to nutrient-rich conditions (Berendse & Elberse 1990). Moreover, adaptation to low-P sites requires different plant features than adaptation to low-N sites (Tilman 1985).

Case studies illustrate clearly how nutrient availability affects the species composition of plant communities. High species densities are associated with interspecific competition for nutrients, and occur particularly at moderate nutrient availability and low biomass production (summer above-ground biomass c. 100–500 g dry wt m⁻²). At fertile sites with high biomass production (summer above-ground biomass >1200 g dry wt m⁻²), there is exclusion of short species by taller species through competition for light. Under conditions of competition for light there is little niche differentiation and as a result the vegetation is species-poor (Grime 1979; Tilman 1985; Moore & Keddy 1989).

In addition to site fertility, the nature of nutrient limitation (N vs. P limitation) has been reported to affect the species composition of the vegetation. The addition of P in the absence of N encourages particularly the growth of leguminous species, that are capable of dinitrogen fixation. In contrast, applications of N in the absence of P has been reported to stimulate the growth of grass species in particular (DiTomasso & Aarsen 1989).

In individual plants, nutrient limitation is recognized by an increase in growth in response to an addition of the limiting nutrient. According to Von Liebig’s Law of the Minimum (Von Liebig 1840), site fertility to individual plants is governed by the availability of the limiting nutrient. Other nutrients are available in relative abundance and are less important for plant growth.

At the community level the analogous response to an addition of the limiting nutrient is an increase in total primary production (Chapin, Vitousek & Van Cleve 1986). Reviews show that community biomass production is usually controlled by N and P. K limitations have been reported only occasionally (DiTomasso & Aarsen 1989; Morris 1991; Vitousek & Howarth 1991; Koerselman & Verhoeven 1995). In a multi-species community, however, plant species may co-exist that are differentially limited by N and P. A site where certain species encounter severe P-deficiency may be P-rich to species that have special adaptations for P uptake (cf. DiTomasso & Aarsen 1989; Verhoeven, Klemmers & Koerselman 1993). This niche differentiation is expected to increase the species richness of natural vegetation (Tilman 1985).

Traditionally, the factor that limits plant growth at a community level is established in a factorial fertilizer experiment with major plant nutrients N, P and K (Chapin et al. 1986). Although performing a fertilization experiment is the most certain way to establish the limiting nutrient, such experiments are time consuming, laborious and disturbing to the site. Thus, it would be beneficial to have a tool that gives the same information as a fertilization experiment, but faster, cheaper and with less disturbance.

In this paper we show that the nature of nutrient limitation can be directly established from the N:P ratio in plant tissue. The ‘N:P tool’ is conceptually simple and accurately predicts the limiting nutrient for plant growth on a community level in a variety of European freshwater wetlands. The N:P tool is of diagnostic value, and its use may solve current scientific debate and practical dilemmas in various research fields.

Rationale and general methods

Hypotheses

We postulated that the ratio of N, P and K in plant tissue gives an indication of the relative availability of these nutrients in the soil. As N and P are most often the limiting factors for plant growth, the research focused on those two elements. We assumed that under conditions of relatively low P supply and high N supply, plants take up more N than P. Due to the luxury consumption of N, the N:P ratio in plant tissue will be relatively high. In contrast, under conditions of relatively high P supply and low N supply, we expect a lower N:P ratio in plant tissue (cf. Shaver & Melillo 1984; Redente, Friedlander & McLendon 1992; Koerselman 1992). Thus, we hypothesized that plant species have a ‘critical’ N:P ratio, that tells us whether growth of the species is N-limited or P-limited. In this paper, we test this hypothesis at the level of plant communities, i.e. that the N:P ratio of bulk vegetation samples indicates the nature of nutrient limitation at the community level (P vs. N limitation). In addition, we discuss whether plant species differ in their relative N and P requirements, and thus have different critical N:P ratios.

Elemental ratios have been successfully used to establish the nature of nutrient limitation in aquatic ecology (e.g. Redfield, Ketchum & Richards 1963; Rhee 1978; Smith 1982; Downing & McCauley 1992) and in agricultural sciences (e.g. Tisdale, Nelson & Beaton 1985). In terrestrial ecology, however, this approach has been largely ignored (but see Wassen 1990; Koerselman 1992).

Data and analyses

Vegetation N:P ratio and the nature of nutrient limitation at a community level

To test the hypothesis that the vegetation N:P ratio indicates the nature of nutrient limitation at the community level (P vs. N limitation) we reviewed fertilization studies in which both community biomass response following nutrient additions and plant tissue nutrient concentrations in unfertilized control plots were recorded. For practical reasons, we restricted our
literature survey to European freshwater wetlands, including rich fens, poor fens, bogs, wet heathlands, dune slacks and wet grasslands. The variety of wetland ecosystems sampled should give a general applicability to the results.

We selected nutrient enrichment experiments under field conditions with intact plant communities, but also included two studies using a test plant (‘phytometer’) that was grown on enriched soil substratum (Loach 1968; Boyer & Wheeler 1989). Although phytometer experiments do not yield conclusive evidence on the nature of nutrient limitation under field conditions, their design is adequate for studies on the relationship between plant tissue N:P ratios and the nature of nutrient limitation.

Fertilization studies were selected using the following criteria.

1. Plant growth was either limited by N or by P, by N and P together, or by N or P in co-limitation with K. Studies where K was primarily limiting plant growth were omitted from the database. In studies in which no inferential statistics were applied, we considered a response significant if the relative response to a treatment was greater than 1:25.

2. Appropriate experimental design. (a) The experimental design assessed single-nutrient effects (including N and P vs. control), single vs. combined nutrient effects (incl. N, P and NP vs. control), or, the best case, all single and combined effects (factorial design, usually with N, P and K). As an exception to this condition, one study was included that assessed only the effect of various P gifts on biomass production (Boyer & Wheeler 1989). In this case, the biomass response to P addition alone was so large (factor c. 6) that this was considered adequate proof for P limitation.

(b) In wet ecosystems, water soluble fertilizers may be leached readily from the experimental plot if applied before the onset of the growing season. This risk is particularly high for N, which is poorly adsorbed onto the soil matrix. In addition, N may be lost from the ecosystem owing to denitrification. If fertilizer additions result in increased nutrient availability to the vegetation, they should either result in (i) increased plant growth or (ii) an increase of plant tissue nutrient concentration. Studies where nutrient additions did not produce any of these two responses were omitted from the database, as we felt that the experimental design was inadequate.

3. Plant tissue analyses of N and P were performed in unfertilized control plots at the time of harvest.

A literature survey including international journals, as well as scientific reports revealed that in total 40 studies in a variety of wetland ecosystems met the above criteria. The set of studies presented in Table 1 were all carried out in areas with a vegetation of perennial herbs among which grasses or Cyperaceae were often dominant and the groundwater table was usually within 0-7 m of the soil surface. They were used for further analyses of the relationship between the N:P ratio of the vegetation and the nature of nutrient limitation.

Based on the biomass response to nutrient additions, each of the 40 wetland sites was classified into one of the following categories: (1) P-limited, (2) N-limited, (3) co-limited by N and P, (4) co-limited by N and K, and (5) co-limited by P and K.

Vegetation N:P ratios reported here are based on total nutrient contents in biomass samples of unfertilized control plots at the moment of harvest. N:P ratios thus represent average values for the community; they are calculated as mass.

Variation of N:P ratios in dune slack species

We selected a subset of the data (dune slacks; Table 1) for further study to examine between-site intraspecific variation, and within-site interspecific variation in nutrient contents and N:P ratios. The combined results of the fertilization studies and the dune slack study are used to discuss interspecific differences in critical N:P ratios, and within-site interspecific variation in the nature of nutrient limitation.

We studied N and P contents, and N:P ratios in five dune slack species in 18 dune slacks along the Dutch coast, in some of which a fertilization experiment was performed simultaneously to detect which nutrient controlled community biomass production (Koerselman & Meuleman 1994). The species selected were Calamagrostis epigejos, Phragmites australis, Lycopus europaeus, Mentha aquatica and Eupatorium cannabinum.

Above-ground biomass samples were collected in August, at peak biomass, from vegetation stands where the selected plant species grew in close proximity. At each site, three sub-samples were collected per species.

The sub-samples were mixed and dried (70°C for 48 h). Total N and P content in plant tissue was determined by acid digestion (340°C) of ground plant material with a mixture of salicylic acid and sulphuric acid using a selenium mixture as catalyst (a modification of the Kjeldahl method; Page, Miller & Keeney 1982). The nitrogen and phosphorus concentration in the digests were determined colorimetrically using the ammonium molybdate method for phosphorus and the indophenol blue method for nitrogen.

Results and discussion

THE N:P RATIO AS INDICATOR OF THE NATURE OF NUTRIENT LIMITATION ON A COMMUNITY LEVEL

Figure 1 shows N and P contents in unfertilized control plots for the following categories: (i) sites where
Table 1. Sites included in this study (n = 40)

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Number of studies</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td>(a) Bogs (n = 3)</td>
<td></td>
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<tr>
<td>Mörhults Mosse (South Sweden)</td>
<td>1</td>
<td>Tamm (1954)</td>
</tr>
<tr>
<td>Stordalen (north Sweden)</td>
<td>1</td>
<td>Aerts et al. (1992)</td>
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<tr>
<td>Akhult (south Sweden)</td>
<td>1</td>
<td>Aerts et al. (1992)</td>
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<td>(b) Poor fens (n = 5)</td>
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<tr>
<td>Biebrza valley (NE-Poland)</td>
<td>1</td>
<td>Verhoeven et al. (1994)</td>
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<tr>
<td>Molenpolder (Vechtflomen, NL)</td>
<td>1</td>
<td>Verhoeven &amp; Schmitz (1991)</td>
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<tr>
<td>’t Hol (Vechtflomen, NL)</td>
<td>1</td>
<td>Verhoeven &amp; Schmitz (1991)</td>
</tr>
<tr>
<td>Chopham Common (NE-Hampshire, UK)</td>
<td>1</td>
<td>Loach (1968)</td>
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<tr>
<td>Kismeldon (Devon, UK)</td>
<td>1</td>
<td>Van Oorschot (1996)</td>
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<td>(c) Rich fens (n = 13)</td>
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<td>Buitengoor (Mol, Belgium)</td>
<td>1</td>
<td>Boeye &amp; Verheijen (unpublished)</td>
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<tr>
<td>Goorken (Arendonk, Belgium)</td>
<td>1</td>
<td>Boeye &amp; Verheijen (unpublished)</td>
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<tr>
<td>Zwarte Beek (Hasselt, Belgium)</td>
<td>1</td>
<td>Boeye &amp; Verheijen (unpublished)</td>
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<tr>
<td>Brackloonz Lough (Crossmolina, Ireland)</td>
<td>1</td>
<td>Kooijman (1993)</td>
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<tr>
<td>Biebrza valley (NE-Poland)</td>
<td>2</td>
<td>Verhoeven et al. (1994)</td>
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<tr>
<td>Westbroek (Vechtplassen, NL)</td>
<td>1</td>
<td>Vermeer (1986a)</td>
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<td>Gagelpolder (Vechtplassen, NL)</td>
<td>1</td>
<td>Vermeer (1986b)</td>
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<tr>
<td>Groot Zandbrink (Gelderse Vallei, NL)</td>
<td>1</td>
<td>Vermeer (1986b)</td>
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<tr>
<td>Zwartebroek (Gelderse Vallei, NL)</td>
<td>1</td>
<td>Vermeer (1986b)</td>
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<tr>
<td>Westbroek (Vechtplassen, NL)</td>
<td>1</td>
<td>Verhoeven &amp; Schmitz (1991)</td>
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<tr>
<td>Badley Moor (Norfolk, UK)</td>
<td>1</td>
<td>Boyer &amp; Wheeler (1989)</td>
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<tr>
<td>Valley of Reuss (Zürich, Switzerland)</td>
<td>1</td>
<td>Egloff (1983)</td>
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<td>(d) Wet heathlands (n = 3)</td>
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<tr>
<td>Chopham Common (NE-Hampshire, UK)</td>
<td>2</td>
<td>Loach (1968)</td>
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<tr>
<td>Kruishaarse Heide (N-Brabant, NL)</td>
<td>1</td>
<td>Aerts &amp; Berendse (1988)</td>
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<td>(e) Wet grasslands (n = 7)</td>
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<tr>
<td>Veenkampen (Wageningen, NL)</td>
<td>1</td>
<td>Oomes (1995)</td>
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<tr>
<td>Born-Zuid (Wageningen, NL)</td>
<td>1</td>
<td>Bloemhof (unpublished)</td>
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<tr>
<td>Ossekkampen (Wageningen, NL)</td>
<td>1</td>
<td>Bloemhof (unpublished)</td>
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<td>Drentse Aa (Groningen, NL)</td>
<td>4</td>
<td>Olff (1992)</td>
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<td>(f) Dune slacks (n = 9)</td>
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<tr>
<td>Berkheide (Katwijk, NL)</td>
<td>1</td>
<td>Koerselman &amp; Meuleman (1994)</td>
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<tr>
<td>Meijendel (Den Haag, NL)</td>
<td>1</td>
<td>Koerselman &amp; Meuleman (1994)</td>
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<tr>
<td>Noordhollands Duinreservaat (Castricum, NL)</td>
<td>5</td>
<td>Koerselman &amp; Meuleman (1994)</td>
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<tr>
<td>Verlakkervallei (Schouwen, NL)</td>
<td>1</td>
<td>Koerselman &amp; Meuleman (1994)</td>
</tr>
<tr>
<td>Kennemerduinen (Haarlem, NL)</td>
<td>1</td>
<td>Koerselman &amp; Meuleman (1994)</td>
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</table>

Fig. 1. Relationship between vegetation N and P content and the nature of nutrient limitation in 40 European wetlands (bogs, poor fens, rich fens, wet heathlands, wet grasslands and dune slacks). Data points are from experiments showing evidence for each type of nutrient limitation, as determined by fertilization experiments (see Table 1 for data sources). Nutrient contents shown were determined in unfertilized control plots. Dashed lines depict N:P ratios of 14 and 16, by mass.
fertilization experiments were interpreted as evidence for P-limitation, (ii) sites where N-limitation occurred, (iii) sites where plant growth was co-limited by N and P, and (iv) sites where co-limitation by N and K was observed. The dataset did not contain sites where results of a fertilization experiment indicated co-limitation by P and K. Three main conclusions emerge from the data in Fig. 1.

First, the vegetation N:P ratio clearly discriminates between N- and P-limited sites (Fig. 1). At N:P ratios >16, community biomass production is P-limited. At N:P-values <14, N limits plant growth in all but one study. At N:P ratios between 14 and 16, either N or P may limit plant growth or both elements are equally limiting (‘co-limitation’). All three sites that appeared co-limited by N and P have N:P ratios in the range 14–16. Only in one out of 40 studies in which N or P was established as a limiting nutrient in a fertilization experiment, does the use of critical N:P ratios lead to a false indication. This ‘outlier’ is a species-rich rich fen community studied by Vermeersch (1986a) in which N controlled plant growth while the vegetation N:P ratio was 20.

In conclusion, Fig. 1 strongly supports our hypothesis that the N:P ratio accurately predicts the nature of community nutrient limitation in a variety of freshwater wetlands.

A second point of interest is the large variation in N content (ranging from 6 to 20 mg N g⁻¹ dry wt) and particularly P content (0.2–3.3 mg P g⁻¹ dry wt) that emerges from Fig. 1. This variation is most likely to reflect differences in the supply ratio of N and P rather than differences in absolute N and P availability.

Shaver & Melillo (1984) demonstrated that plants may regulate their N and P balance only to a certain extent. The N and P contents of Carex laevis, Carex aquatilis, and Typha latifolia varied two- to four-fold when exposed to growth media with inorganic N:P supply ratios ranging from 0:8–61. Moreover, the N:P ratio in the plants was strongly correlated with the N:P supply ratio.

If the observed variation in N and P contents of wetland vegetation were due to differences in absolute N and P availabilities, we would expect fertile sites to have higher nutrient contents in plant tissue than infertile sites. In the absence of data for nutrient availability at the sites, we used above-ground summer biomass as an index of site fertility. This parameter was determined in 36 of the 40 studies that we reviewed. Figure 2 clearly shows that the vegetation at fertile sites (high biomass) does not have higher N and P contents than the vegetation at infertile sites (low biomass). The correlation between summer biomass and plant tissue nutrient contents is very poor, both for the whole dataset (Fig. 2a,b) and for parts of it [N content vs. biomass for N-limited sites and P content vs. biomass for P-limited sites (Fig. 2c,d)].

From the study by Shaver & Melillo (1984) and the data in Fig. 2 we conclude that the N and P content in plant tissue is mainly determined by the supply ratios of N and P, e.g. a high N content reflects situations where high N is available relative to P. In such situations, the absolute N availability is not necessarily high. Presumably, absolute N and P availability mainly affects biomass production, and the species composition of the vegetation rather than N and P content in plant tissue.

A third conclusion that emerges from Fig. 1 is that no clear relationship exists between the nutrient content in plant tissue and the nature of nutrient limitation. In wet grasslands N controlled plant growth at relatively high concentrations of c. 20 mg N g⁻¹ dry wt [Olliff 1992; Oomes 1995; Bloemhof (in prep.)], whereas it did not limit plant growth in wet heathlands and rich fens at much lower concentrations of c. 10 mg N/g dry wt (Loach 1968; Aerts & Berendse 1988; Boyer & Wheeler 1989). The pattern for P is more complex. Data indicate that a threshold concentration exists (1.1 mg P g⁻¹ dry wt) above which P will not limit plant growth (see also Fig. 2b,d). At concentrations below this threshold, however, P is not necessarily controlling plant growth (Vermeersch 1986a,b; Koerselman & Meuleman 1994; Verhoeven et al. 1994).

Thus, it is the ratio between N and P that indicates whether N or P limits plant growth, not the absolute N and P content in plant tissue.

DO PLANT SPECIES HAVE IDENTICAL CRITICAL N:P RATIOS?

Figure 1 proves that critical N:P ratios exist for wetland communities. This, however, does not prove indisputably that all wetland plant species within the communities studied have identical relative N and P requirements, and thus identical critical N:P ratios. Interspecific differences in critical N:P ratios may have been masked in our study, as we related the average N:P ratio of a multi-species vegetation to the nature of nutrient limitation at the community level.

A clear test of the hypothesis that wetland plant species have identical critical N:P ratios requires data from experiments in which populations of species with different N:P ratios are exposed to additions of N and P, and subsequent growth responses are recorded. Unfortunately, such data are not available, preventing an unequivocal test of the hypothesis.

However, circumstantial evidence suggests that interspecific differences in critical N:P ratio are likely to be insignificant. Figure 1 includes a large variety of vegetation types and plant species. It is highly unlikely that corporate critical N:P ratios would have emerged from the data if interspecific differences in critical N:P ratios among plant species were significant at these sites, because at least 11 of the 40 sites included in our study were near-monocultures, where only one species accounted for over 80% of total biomass, viz. Erica
Fig. 2. Relationship between above-ground summer biomass (g m$^{-2}$) and vegetation nutrient content (mg g$^{-1}$ dry wt) in unfertilized control plots in wetlands where the nature of nutrient limitation of the community was established in a fertilization experiment. Data sources are given in Table 1. (a) Biomass vs. vegetation N content for all sites where biomass readings were available ($n = 36$). (b) Biomass vs. vegetation P content for all sites where biomass readings were available ($n = 36$). (c) Biomass vs. vegetation N content for all sites where biomass readings were available and N (co)-limited community biomass production ($n = 27$). (d) Biomass vs. vegetation P content for all sites where biomass readings were available and P (co)-limited community biomass production ($n = 12$).

However, the evidence in favour of the assumption that plant species do not significantly differ in respect of their optimal N:P ratio is circumstantial and a rigorous test of this hypothesis is required.

**Variation in Nutrient Content and N:P Ratio Among Species Occupying Dune Slack Sites**

In the dune slack study we observed huge within-site interspecific variation in N:P ratio among five plant species (Fig. 3). Between-site intraspecific ranges of N content, P content and N:P ratio were also large, but about equal for the five plant species (Table 2); they encompassed almost the total range of these parameters depicted in Fig. 1. Between-site and within-site variation in N and P content is well known from other studies (e.g. Boyd 1978; Ohlson 1988; Hayati & Proctor 1991).

Between-site intraspecific variation once more illustrates the plasticity of plant species with respect to N and P contents, probably in response to differences in N and P supply ratios (Shaver & Melillo 1984).

Within-site interspecific variation in N:P ratios can be explained from differences in nutrient uptake mechanisms between species or differences in rooting depth. For example, Phragmites australis usually has a considerably higher N:P ratio than other species (Fig. 3) and through deep rooting Phragmites australis probably exploits larger soil compartments than the other species, which exploit mainly the upper soil compartments.

If we accept the suggestion presented in the foregoing section that interspecific differences in critical N:P ratio may be insignificant, we must conclude that at sites 1, 2 and 4 species co-occur that are differentially limited by N or P (Fig. 3).

Fertilization studies showed that community biomass production at site 4 is P-limited, whereas N controls community biomass production at the other four sites (Koerselman & Meuleman 1994). Within the plant communities of three of these sites we find plant species with N:P ratios indicating that their growth is controlled by an element that does not control community biomass production (Phragmites australis and Calamagrostis epigejos at site 1, Phragmites australis at site 2, and Calamagrostis epigejos, Lycopus europaeus, Mentha aquatica and Eupatorium cannabinum at site 4). The species were not important constituents of the vegetation, and therefore did not contribute significantly to community biomass and bulk vegetation N:P ratios.


![Fig. 3. Vegetation N:P ratios (mg mg⁻¹) and N:P ratios in Phragmites australis, Lycopus europaeus, Mentha aquatica, Calamagrostis epigejos and Eupatorium cannabinum in five Dutch dune slacks. The plant species were not important constituents of the vegetation at these sites. Vegetation N:P ratios refer to the bulk vegetation samples from unfertilized control plots of fertilization experiments by Koerselman & Meuleman (1994).](image-url)
Our assumption that within plant communities the growth of individual species can be limited by different nutrients is supported by experimental data reviewed by DiTomasso & Aarson (1989). The co-existence of plant species that are differentially limited by N and P helps explain the common observation that community biomass production in a multi-species plant community is increased particularly by the addition of one element (being ‘primarily limiting’ to plant growth), but also to a lesser extent by other elements (‘secondarily’ and ‘tertiarily’ limiting on the community level, respectively). These other elements are probably primarily limiting growth of non-dominating species within that community.

**CONSTRAINTS AND APPLICATIONS OF THE N:P TOOL**

The use of the N:P tool is a quick and simple alternative to laborious fertilization experiments which could be used at a community level in a wide range of wetland types.

The main drawback to the use of N:P ratios is that they can only be used as an indicator of the nature of nutrient limitation under conditions where either N or P limits plant growth. As K seldom limits plant growth (Koerselman & Verhoeven 1995; DiTomasso & Aarson 1989), the risk of misinterpretation is, however, small. As more data on K limitation becomes available, we can establish critical N:K and K:P ratios as well. This will aid diagnosis of the order in which N-P-K limit plant growth, following methods such as those described by Tisdale et al. (1985).

Another limitation of the N:P tool is that it does not indicate the absolute nutrient availability at the site, only the N and P supply ratio. This drawback can be partly overcome if the N:P tool is combined with data on biomass to produce an index of site fertility based on N and P stocks in biomass (g N m⁻², g P m⁻²).

As nutrient limitation is a driving force in ecosystem succession, use of the N:P tool may increase our understanding of numerous facets of physiological, population, community and ecosystem ecology. As an illustration, we give four examples from various research fields.

1. The use of the N:P tool may increase greatly our limited knowledge of the nature of nutrient limitation in various ecosystem types (DiTomasso & Aarson 1989; Vitousek & Howarth 1991). This may be particularly useful in remote and inhospitable areas, as information can be gained during very short summer field trips. In combination with data on summer biomass, the N:P tool can be used to estimate P and N availability of sites (g N m⁻², g P m⁻²).

2. The N:P tool can be used in restoration projects aiming at a reduction of site fertility, as this requires a reduction of the availability of the nutrient that controls plant growth (Koerselman & Verhoeven 1995). Often, reducing P availability requires different measures than reducing N availability. The use of the N:P tool may help to determine the most efficient way to reduce the site fertility. For restoration purposes, however, it is important to have an insight into interspecific differences in N:P ratio among plant species at the restoration site. If such variation occurs, and if plant species do have similar critical N:P ratios, certain measures to reduce site fertility may not affect all species to the same extent. Thus, apart from reducing biomass production, measures may also affect the species composition of the vegetation (see Koerselman & Verhoeven 1995).

3. The N:P tool can be used to test Tilman’s theory (Tilman 1985), that predicts maximum species density under circumstances where N- and P-limited species may co-exist, viz. when N and P co-occur as limiting resources at the community level. A test of Tilman’s theory is of interest to nature conservation, where the aim is often to increase species richness.

4. Finally, the N:P tool can be used to test the hypothesis by Vitousek & Walker (1987) that a shift from N limitation towards P limitation occurs during primary ecosystem succession, as P availability in soils essentially declines through the course of soil development, while N availability increases with humus accumulation.

**Concluding remarks**

From the data presented here, we conclude that the vegetation N:P ratio can accurately predict the nature of nutrient limitation at a community level. The variety of wetland ecosystems included in our study warrants a general applicability of the critical N:P ratios (14 and

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**Table 2. Range in plant tissue N and P content (mg g⁻¹ dry wt) and N:P ratio in five species that were sampled from Dutch dune slacks**

<table>
<thead>
<tr>
<th>Species</th>
<th>N content</th>
<th>P content</th>
<th>N:P ratio</th>
<th>Number of sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phragmites australis</td>
<td>13-31</td>
<td>1-0-3-1</td>
<td>5-29</td>
<td>11</td>
</tr>
<tr>
<td>Lycopus europaeus</td>
<td>9-35</td>
<td>0-9-3-6</td>
<td>5-25</td>
<td>11</td>
</tr>
<tr>
<td>Mentha aquatica</td>
<td>9-30</td>
<td>0-9-3-6</td>
<td>4-18</td>
<td>14</td>
</tr>
<tr>
<td>Calamagrostis epigejos</td>
<td>9-22</td>
<td>0-8-2-4</td>
<td>5-33</td>
<td>17</td>
</tr>
<tr>
<td>Eupatorium cannabinum</td>
<td>13-26</td>
<td>1-1-3-8</td>
<td>5-29</td>
<td>10</td>
</tr>
</tbody>
</table>
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16 for N and P limitation, respectively) to herbaceous freshwater wetlands. As critical N:P ratios are suc-
sessfully used to establish the nature of nutrient limit-
tation in aquatic and agricultural ecosystems (e.g. Redfield et al. 1963; Rhee 1978; Smith 1982; Tisdale
et al. 1985; Downing & McCauley 1992), the general
concept may be applicable to a much wider range of
ecosystems. As illustrated above, the N:P tool is of
diagnostic value in various research fields.

There is circumstantial evidence suggesting that
interspecific differences in critical N:P ratios among
species may be insignificant. However, further
research on this issue is strongly recommended.

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