

SPECIES RICHNESS–PRODUCTIVITY PATTERNS DIFFER BETWEEN N-, P-, AND K-LIMITED WETLANDS

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Abstract. We evaluated whether the kind of nutrient limitation (N, P, or K) may affect species richness–productivity patterns and subsequently may explain variation in species richness and in richness of threatened species. We present a data set from previous studies in wetlands in Poland, Belgium, and The Netherlands and examine species richness–productivity patterns for vascular plants in all 150 sites together as well as for N-, P-, and K-limited sites separately. The kind of nutrient limitation was assessed by N:P, N:K, and K:P ratios in the vegetation. Critical values for these ratios were derived from a literature review of fertilization experiments. The kind of nutrient limitation influenced species richness–productivity patterns in our 150 sites through large differences in productivity. P (co)-limitation occurred only at low productivity, K (co)-limitation up to intermediate productivity, and N limitation along the entire productivity gradient. There was a decreasing trend in species richness with increasing productivity for K (co)-limited sites, whereas for both the N-limited sites and P (co)-limited sites a sort of “filled hump-shaped curve” was observed. The species richness–productivity relationship for threatened species was restricted to a much narrower productivity range than that for all species. Richness of threatened species was higher in P (co)-limited sites than in N-limited sites, suggesting that increased P availabilities in wetlands may be particularly important in causing disappearance of threatened species in western Europe. The role of nutrient limitation in species richness–productivity relationships not only reveals mechanisms that may explain variation in species richness and occurrence of threatened species, but it also may be important for nature management practice.

Key words: biodiversity; hump-shaped curve; limiting resources; nutrient limitation; productivity–diversity relationships; species diversity; species richness.

INTRODUCTION

An important factor for variation in species richness at the local scale is its relationship with productivity (e.g., Grace 1999). Grime (1979) described the species richness–productivity relationship as a hump-shaped curve, with low species richness at low and high productivity. The shape of the curve occurs because only a few species are adapted to extremely nutrient-poor conditions and a few dominant species outcompete all others at high resource levels. Studies in which a wide range of plant communities were included have supported the hump-shaped curve, and they have also demonstrated that not only maximum species richness but also maximum variation in species richness occurs at intermediate productivity levels (Grime 1979, Vasander 1982, Moore et al. 1989, Wheeler and Shaw 1991, Grace 1999).

Differences among species in their abilities to exploit limiting resources affect the coexistence of species (Tilman 1982). Since some plant species have special adaptations to low availabilities of nitrogen, e.g., symbiotic N₂-fixation (Tilman 1982), and others to low

availabilities of phosphorus, e.g., root secretion of phosphatases or chelates (Vitousek and Howarth 1991, Hinsinger 2001), the kind of nutrient limitation may affect species composition. The kind of nutrient limitation also may affect species composition and richness through its effect on productivity, as especially maximum productivity levels that can be attained may differ among N-, P-, or K-limited sites (Olde Venterink et al. 2001a). In the present study we will examine whether influences of limitation type on species richness–productivity relationships can be observed in the field for a wide range of plant communities.

For conservation of biodiversity it is essential to know whether site conditions promoting a high general species richness will also be beneficial for the maintenance of threatened species. Species richness–productivity relationships for rare and/or threatened species in Canadian and British wetlands showed hump-shaped patterns with a narrow hump at low productivity (Moore et al. 1989, Wheeler and Shaw 1991). The narrow hump indicates that these species are sensitive to productivity increases and hence to increased availabilities of limiting nutrients. Considering the strong increase in atmospheric N deposition in the industrialized parts of the world (Holland et al. 1999), one tends to think that species adapted to a low N availability and N limitation have become threatened in

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these areas. Therefore, we also will examine whether the kind of limitation affects species richness–productivity relationships for threatened species separately.

The present field evaluation of species richness–productivity patterns was organized along three questions. First, we asked whether maximum species richness levels differ among sites where N, P, or K is the limiting nutrient. Second, we asked whether species richness–productivity patterns are affected by the relationship between the limiting nutrient and the maximum productivity level that can be attained. Third, we asked whether the relationship between the limiting nutrient and species richness–productivity pattern is different for common species vs. threatened species. We analyzed data on productivity and species richness of vascular plants from 150 sites, 76 in fairly undisturbed herbaceous wetlands in Poland and 74 in relatively disturbed herbaceous wetlands in Belgium and The Netherlands. The data set included data from our previous published and unpublished studies in these areas (Wassen et al. 1990, 1995, De Mars et al. 1996, Olde Venterink et al. 2001b, 2002b). Earlier studies in herbaceous wetlands showed hump-shaped curves and “clouds of points” both for overall plant species richness and for threatened plant species (e.g., Moore et al. 1989, Wheeler and Shaw 1991, Grace 1999). Moreover, herbaceous wetlands can be growth limited by N and P as well as K (Verhoeven et al. 1996b, Olde Venterink et al. 2001a).

In order to determine the kind of nutrient limitation at our 150 sites, we compared N:P, N:K, and K:P ratios in the aboveground vegetation with critical ratios. Critical nutrient ratios were derived from data of 44 fertilization experiments in literature.

METHODS

Determination of N, P, and K limitation

The ratio of N:P in plant tissue is considered a useful predictor to determine whether growth is limited by N or P (e.g., Ingstad 1979, Shaver and Chapin 1995, Bedford et al. 1999). Moreover, Wassen et al. (1995) and Koerselman and Meuleman (1996) used N and P concentrations in aboveground vegetation of the control sites of fertilization experiments to determine critical N:P ratios. However, K also has been shown to (co)-limit growth in bogs (Goodman and Perkins 1968), fens (Boeye et al. 1997, Van Duren et al. 1997a), and wet meadows (Vermeer 1986, Olf 1992, Oomes 1995, Pegtel et al. 1996, Van Duren et al. 1997b, Olde Venterink et al. 2001a). Ratios of N:K or K:P are less regularly used than N:P ratios, and critical values for these ratios presented by Pegtel et al. (1996) and Ertsen (1998) differ considerably and were not based on fertilization experiments. We therefore determined the critical values for N:K and K:P ratios from unfertilized control plots of fertilization experiments found in literature.

We applied the following criteria in selecting studies on which to base development of critical values for N:P, N:K, and K:P ratios: (1) fertilization experiments were carried out in herbaceous wetlands or grasslands; (2) fertilization treatments included at least N, P, K, and N+P+K treatments and an unfertilized control; (3) N, P, and K concentrations in aboveground biomass of vascular plants in the control treatment were presented, or concentrations found in aboveground biomass could largely be ascribed to those in vascular plants because bryophytes were absent or rare; (4) fertilization with N+P+K resulted in a significantly ($P < 0.05$) higher biomass than the control, to make sure that the vegetation was growth limited by nutrients instead of other factors; (5) only fertilization *addition* experiments were obtained to avoid bias from differences between addition and omission experiments (cf. Olf 1992); (6) effects of fertilization were determined on total aboveground vegetation or aboveground vascular plants; experiments with single species were used only if it was shown that the species made up more than 75% of the vegetation (e.g., Tamm 1954, Goodman and Perkins 1968, Loach 1968). The selected studies are shown in Appendix A.

Second, we calculated N:P, N:K, and K:P ratios (in milligrams per milligram) in aboveground biomass of vascular plants of the control plots of the reported fertilization experiments. We subsequently tested whether these ratios were significantly different among sites growth limited by different nutrients (as determined by the outcome of the fertilization experiments).

Third, in order to determine critical N:P, N:K, and K:P ratios, we constructed a triaxial diagram in which the type of nutrient limitation (outcome of the fertilization experiments) is plotted against the ratio of N:P:K in the vegetation.

Productivity and species richness data

Data from the 150 sites in Poland, Belgium, and The Netherlands are presented in Appendix B. These sites were all unfertilized and were used to establish species richness–productivity patterns. They include information on aboveground biomass of vascular plants, the N, P, and K concentrations in the biomass, and the species richness of all vascular plants and threatened vascular plant species. The data set combines 76 sites in bogs, poor fens, rich fens, and wet meadows in the Biebrza catchment (northeast Poland; data from Wassen et al. [1990, 1995], De Mars et al. [1996]; M. J. Wassen [*unpublished data*]) with 74 sites in poor fens, rich fens, and wet meadows in the Zwarte Beek catchment (northeast Belgium) and the Dommel catchment (southeastern Netherlands; data from Olde Venterink et al. [2001b] and H. Olde Venterink [*unpublished data*]). The Polish and Dutch/Belgian sites differed in the amount of atmospheric N inputs and the annual management regime. Atmospheric N deposition is ~5–10 kg N·ha⁻¹·yr⁻¹ at the Polish sites and 40–50 kg

$\text{N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ at the Dutch and Belgian sites (Verhoeven et al. 1996a, Olde Venterink et al. 2002b). Most Dutch/Belgian sites (83%) and some Polish sites (18%) are mown annually.

Standing aboveground biomass of vascular plants at peak biomass during the growing season was used as measure for productivity. It was sampled mid-July 1990 and 1992 (Poland) and mid-July 1995 and 1996 (Belgium, The Netherlands). At every site, three subplots (mostly 50×50 cm, occasionally 30×30 cm) were cut near the soil surface. Litter on the soil surface or woody plant materials were not included in the biomass estimate. Our estimate of productivity is an underestimate of annual net aboveground productivity at low production because we did not include bryophyte production (cf. Pałczynski and Stepa 1991, Wassen et al. 1995). Also, we did not account for biomass turnover (cf. Berendse and Aerts 1987). Dry masses of the vegetation samples were determined after drying at 70°C . N, P, and K concentrations were measured after Kjeldahl digestion of ground plant material. N contents of the digests were determined by the indophenol-blue method using a Skalar autoanalyzer (Skalar, Breda, The Netherlands). P and K contents of the digests were determined by inductively coupled plasma technique (Belgian and Dutch sites), or P was determined by the molybdenum-blue method using the autoanalyzer, and K was determined by flame emission spectroscopy (Polish sites).

At the sites where biomass was harvested, species composition also was recorded in 4-m^2 plots at the Belgian and Dutch sites and in 10-m^2 plots at the Polish sites. To evaluate whether the difference in plot size may have affected species richness measurements (cf. Pastor et al. 1996, Weiher 1999), we re-recorded 13 of the 4-m^2 sites at a 10-m^2 scale, 1–2 yr after the first recording (range of the first recording: 3–35 species). The re-recording generally showed only 0–2 additional species (data not shown), indicating that variation among our 150 sites due to differences in plot size was of minor importance. The number of threatened species was determined for every site, using the “red list” of threatened species for The Netherlands (Van der Meijden et al. 1991). Only actually threatened species on this list (species that have disappeared in at least 25% of map units [1 unit = 25 km^2] compared to an historical reference) were included. Thus species that are rare because of a limited geographical distribution were not included.

Statistics

Significant differences ($P < 0.05$) in N:P, N:K, and K:P ratios (derived from the 44 fertilization experiments from literature) among sites growth limited by different nutrients were tested by means of Tukey tests after one-way ANOVA.

To determine the shape of species richness–productivity relationships we used the nonparametric local

regression routine (loess regression; using an interval “span” containing two-thirds of the data points; cf. Harrell [2001]). Because the plots for all sites, N-limited sites, and P (co)-limited sites showed the “usual” large scatter, we also compared the shapes of the curves enclosing the clouds of points in Fig. 3A–C. To assess the maximum species richness values along the productivity gradients we divided the x -axis into 20 equally sized sections and determined the xy pairs with the highest species richness within them. We calculated loess regressions for all sites, as well as for N-limited sites and P (co)-limited sites, separately. Because of differences in maximum productivity, the sizes of the x -axis sections were smaller for Fig. 3C (31.5 g/m^2) than for Fig. 3A and B (71.4 g/m^2).

We used the Levene test for homogeneity of variance to evaluate whether ranges in species richness were significantly ($P < 0.05$) different among N-limited, P (co)-limited, and K (co)-limited groups of sites. If variation among the three groups was significant, we carried out three additional Levene tests to examine differences in variation between N- vs. P-, N- vs. K-, and P- vs. K-limited sites, respectively.

RESULTS

Before presenting the results of our analysis of whether species richness–productivity patterns are affected by the kind of nutrient limitation, first we show the results of our method to determine N, P, and K limitation.

Determination of N, P, and K limitation

The analysis of fertilization experiments found in the literature showed that nutrient ratios in aboveground vascular plants can be used to distinguish (1) N-limited sites, (2) P- or P+N-limited sites, and (3) K- or K + N-limited sites from each other ($P < 0.05$; Appendix A). Nutrient ratios cannot, however, be used to distinguish N + P co-limited sites from P-limited sites ($P = 0.986$), nor can K + N co-limited sites be distinguished from K-limited sites ($P = 0.999$; Appendix A).

In order to determine critical N:P, N:K, and K:P ratios, we plotted the N, P, and K concentrations in vascular plants in a triaxial diagram (Fig. 1). Every point in the diagram represents one fertilization experiment from literature. The nutrient concentrations are from the control plots, and the kind of limitation at the sites (outcome of the fertilization experiments) is indicated by different symbols. The diagram divided the sites into three categories: (1) N-limited sites, (2) P- or P+N-limited sites and (3) K- or K+N-limited sites, and a fourth category for which nutrient ratios cannot be used to determine the kind of nutrient limitation. (Only 8 of the 150 sites of Fig. 2A fell into this fourth category.) With only one exception (“?” in Fig. 1), the triaxial diagram yielded the following critical ratios: (1) N-limited sites, $\text{N:P} < 14.5$ and $\text{N:K} < 2.1$; (2) P- or P+N-limited sites, $\text{N:P} > 14.5$ and $\text{K:P} > 3.4$; (3)

K- or K+N-limited sites, $N:K > 2.1$ and $K:P < 3.4$. These ratios are shown by the three solid lines in the diagram, each crossing one edge of the diagram. For instance, the N:P ratio line crosses the rightside corner. On the opposite axis it crosses the point where $10P = 40.8\%$, $N = 59.2\%$ (to be read on the right axis), and $K = 0\%$ (the horizontal axis) yielding a critical N:P ratio of 14.5. Sites below the line are N limited, sites above the line are P or P + N limited.

Species richness–productivity patterns

Ranges in aboveground biomass of vascular plants (hereafter called productivity; see *Methods*) clearly differed between N-limited, P (co)-limited, and K (co)-limited sites (Fig. 2). P limitation occurred only at low productivity ($<650 \text{ g/m}^2$; Fig. 3C), K limitation up to intermediate productivity ($<1000 \text{ g/m}^2$; Fig. 3D), and N limitation along the entire productivity gradient (Fig. 3B).

Local regression analysis suggested a weak decreasing trend in species richness with increasing productivity in Fig. 3A and B, but the very low R^2 values (0.05 and 0.07, respectively) underlined the large scatter. Local regression analysis resulted in a unimodal curve for the pattern in Fig. 3C, also with a very large variation ($R^2 = 0.27$). The local regression in Fig. 3D illustrated a decreasing trend ($R^2 = 0.80$). Besides local regressions through the clouds of points, we also performed local regressions to assess the shapes of the curves enclosing the clouds of points (see *Methods*). These regressions between productivity and “maximum species richness” resulted in a wide “unimodal” curve for N-limited sites (Fig. 3B, $R^2 = 0.43$) and a narrow “unimodal” curve for P (co)-limited sites (Fig. 3C, $R^2 = 0.72$). The overall pattern was enclosed by a horizontal line at our low-productivity sites and a decreasing line at higher productivity (Fig. 3A, $R^2 = 0.53$).

Threatened species only occurred at low-productivity sites (Fig. 3E). The pattern in Fig. 3G shows a narrow “hump-shaped” curve enclosing a cloud of points. Such patterns can also be observed in Fig. 3E and F, although local regressions assessing the “enclosing curves” resulted in decreasing trends.

Ranges in species richness of all vascular plants were not significantly different ($P > 0.95$) among sites where growth was limited by N, P, or K (Appendix C). In contrast, ranges in richness of threatened species differed between N-limited sites and P (co)-limited sites ($P < 0.05$; Appendix C). N-limited sites only occasionally contained more than two threatened species (Fig. 3F), whereas P (co)-limited sites regularly contained up to five threatened species (Fig. 3G).

DISCUSSION

After evaluating the results of our method to determine N, P, and K limitation, first we discuss the observed relationship between the kind of nutrient limi-

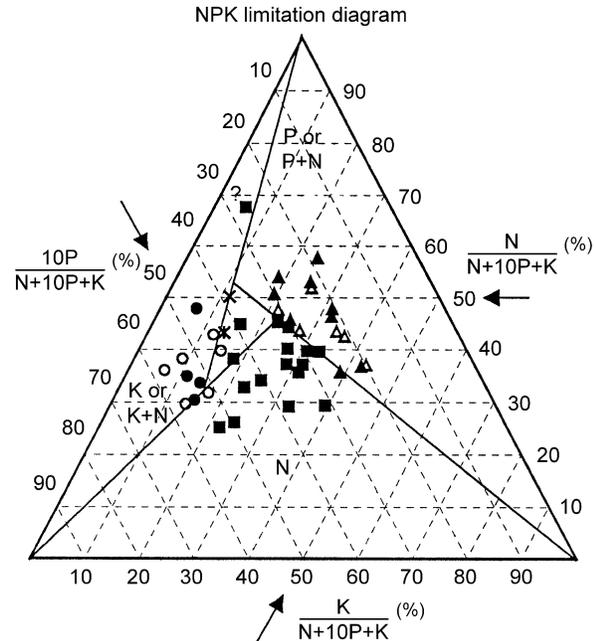


FIG. 1. Triaxial diagram showing the relationship between the ratio of N:P:K in aboveground vascular plants vs. the type of nutrient limitation in 44 European wetlands (3 bogs, 13 fens, 3 wet heathlands, 16 wet meadows, 9 dune slacks). Symbols represent the type of nutrient limitation determined by fertilization experiments: filled squares, N-limited; filled triangles, P-limited; filled circles, K-limited; open triangles, P+N co-limited; open circles, K+N co-limited; \times , P+K co-limited; star (*), N+P+K co-limited. N, P, and K contents are from control plots of the experiments. For visual reasons, P concentrations were multiplied by a factor of 10. Solid lines represent critical ratios of N:P (14.5), N:K (2.1), and K:P (3.4; see *Results*). The lines divide the diagram in four parts: three parts containing sites limited by N, P or P+N, and K or K+N, respectively. For the fourth (central) part of the diagram, nutrient ratios cannot be used to determine the type of nutrient limitation. Arrows show the direction in which the axes should be read (following the dashed lines). References: Tamm (1954), Goodman and Perkins (1968), Loach (1968), Vermeer (1986), Aerts and Berendse (1988), Verhoeven and Schmitz (1991), Olf (1992), Kooijman (1993), Koerselman and Meuleman (1994), Oomes (1995), Boeye et al. (1997), Van Duren et al. (1997a, b), Wassen et al. (1998), Olde Venterink et al. (2001a); M. J. Wassen and J. T. A. Verhoeven (*unpublished data*).

tation and species richness–productivity patterns for all vascular plant species, and second we discuss this relationship for threatened species.

Determination of N, P, and K limitation

Our analysis of fertilization experiments from literature resulted in critical ratios of N:P = 14.5, N:K = 2.1, and K:P = 3.4 in aboveground vascular plants, which can be used to distinguish (1) N-limited sites, (2) P- or P+N-limited sites, and (3) K- or K+N-limited sites from each other. For the N:P ratio there is one important difference with a previous analysis by Koerselman and Meuleman (1996) who derived ratios of

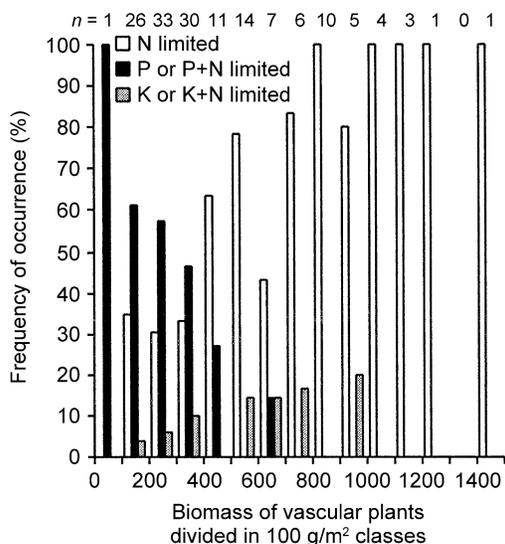


FIG. 2. Frequency of occurrence of N limitation, P (co)-limitation, and K (co)-limitation vs. aboveground biomass of vascular plants in herbaceous wetlands (150 sites of Fig. 3). Because the kind of limitation could not be determined for all sites (see *Results*), the sum of frequencies is not 100% for every biomass class. The abbreviation n = number of sites.

<14 for N limitation, >16 for P limitation, and in between (14–16) for co-limitation by N and P. Our analysis clearly showed that the N:P ratio cannot be used to distinguish N+P co-limited sites from P-limited sites ($P = 0.986$), nor can an N:K ratio be used to distinguish K+N co-limited sites from K-limited sites. Therefore, we use the terms P (co)-limited and K (co)-limited in this study. Both our analysis of fertilization experiments and that of Koerselman and Meuleman (1996) show that solo limitation by P occurs between N:P 14.5 and 16; the difference between the two analyses is caused by additional experiments in our review showing that N+P co-limitation also occurs at N:P > 16 (Appendix A). The importance of deriving critical ratios at sites where the kind of limitation is experimentally determined is demonstrated by the great difference between our N:K and K:P ratios and those derived without a reference to fertilization experiments (e.g., N:K = 1.2 and K:P = 8.6; Pegtel et al. 1996). The preferential use of the three critical nutrient ratios above critical values for single nutrients is illustrated by the N- and/or P-limited sites in Appendix A, where according to the often-used critical K concentration of 8 mg/g (De Wit et al. 1963, Willby et al. 2001), K limitation would have been predicted.

Species richness–productivity patterns at different kinds of nutrient limitation

In this paper we showed that species richness–productivity patterns are different for plant communities that are growth limited by different nutrients, because of a highly significant relationship between the kind of

nutrient limitation and productivity ranges (Fig. 2). A restriction of P (co)-limitation to relatively low-productivity sites was observed in both the Belgian/Dutch sites as well as the Polish sites (Fig. 3). This is in agreement with a previous study evaluating productivity levels of control plots from fertilization experiments (Olde Venterink et al. 2001a).

One explanation for the absence of P (co)-limitation at high-productivity sites may be that most, but not all, of our high-productivity sites were subjected to a form of flooding (Appendix B). Flooded sites may have relatively high P inputs from P adsorbed to riverine sediment (Willby et al. 2001). Alternatively, the absence of P (co)-limitation at high-productivity sites may be due to adaptations of plants to P-limited conditions; e.g., large investments in roots, mycorrhizal associations, and/or production of exudates as organic acids or phosphatases by the roots (cf. Clarkson 1985, Vitousek and Howarth 1991, Neumann et al. 1999). Such investments require considerable amounts of photosynthates (Marschner 1995, Hinsinger 2001) and therefore may limit aboveground biomass levels that can be achieved. Other explanations in literature for the occurrence of P (co)-limitation, such as (1) old successional stages in soil development (Vitousek and Howarth 1991), (2) chemical P adsorption by calcium or iron (Boeye and Verheyen 1994; Verhoeven et al. 1996b), (3) high atmospheric N deposition rates (Aerts et al. 1992), and (4) annual hay-making (Koerselman et al. 1990, Olf and Pegtel 1994), do not give appropriate explanations for absence of P (co)-limitation at our high-productivity sites. All our sites were relatively old successional stages of soil development (i.e., soils had a large accumulation of organic matter, and young quag fens were not included), both the low-productivity and high-productivity sites in Poland were calcium-rich (Wassen et al. 1996), and both the low-productivity and high-productivity Belgian and Dutch sites received very high N deposition rates and were subjected to hay-making for decades (Olde Venterink et al. 2001b, 2002b).

The species richness–productivity pattern for our 150 sites (Fig. 3A) does not contradict the concept of a hump-shaped curve enclosing a cloud of points, such as observed in other grasslands and wetlands (taking into account the absence of extreme low-productivity sites in our data set; Grime 1979, Vasander 1982, Moore et al. 1989, Wheeler and Shaw 1991, Grace 1999). Moreover, the patterns for N-limited and P (co)-limited sites also may possibly be described by “filled” hump-shaped curves, but with a much narrower hump for the P (co)-limited sites than for the N-limited sites as suggested by the regressions between productivity and “maximum species richness” (cf. lines in Fig. 3B and C). The pattern for K (co)-limited sites showed a decreasing trend (Fig. 3D). Dividing the overall data set (Fig. 3A) into the three subpatterns per limitation type implies that maximum productivity levels differ

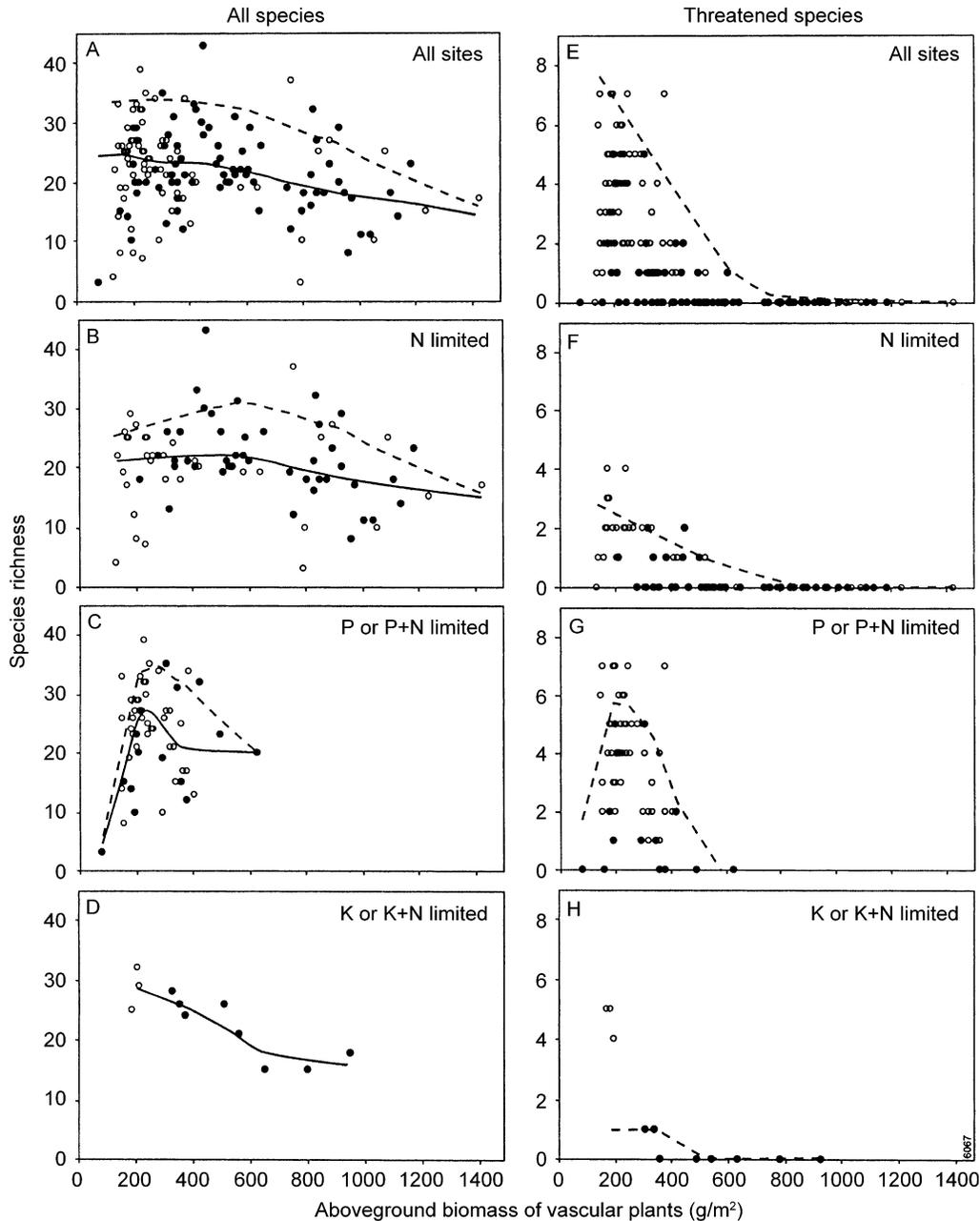


FIG. 3. (A) Species richness of vascular plants and (E) threatened vascular plants vs. aboveground biomass of vascular plants in wetlands in Belgium and The Netherlands (filled circles) or Poland (open circles), as well as the same relationships for (B, F) N-limited sites, (C, G) P (co)-limited sites, and (D, H) K (co)-limited sites. Species richness was recorded at 4 m² (filled circles) or 10 m² (open circles). The type of nutrient limitation was determined by N:P, N:K, and K:P ratios in vascular plants, using critical ratios of Fig. 1. Threatened species are according to the "red list" of plant species in The Netherlands (Van der Meijden et al. 1991). Solid lines show the results of local regressions through the clouds of points in panels (A–D), while dashed lines indicate the shapes of the curves enclosing the clouds of points, as determined by local regression (see *Methods*).

among N-limited, P (co)-limited, and K (co)-limited sites. In general, the main process at high productivity is competitive exclusion for light; i.e., dominance of a few species causing a low species richness (Grime 1979, Huston and DeAngelis 1994). This also may ap-

ply to the highest productive P (co)-limited sites as the vegetation at these sites showed a high cover of sedges and particularly *Molinea caerulea*, i.e., a species known for its capacity to create almost complete dominance (e.g., Bakker and Berendse 1999). However,

Molinia caerulea is never observed at the high productivity levels where, according to the present theory (Grime 1979, Grace 1999), strong dominance is expected and where in our sites (and in British wetlands described by Wheeler and Shaw 1991) the vegetation was dominated by species such as *Glyceria maxima* or *Phragmites australis*. Dominance by different species at N-, P-, or K-limited sites also was observed in the Park Grass experiment at Rothamsted, where differences in nutrient limitation have been created during a century of nutrient additions (Williams 1976, Tilman 1982). Hence, the occurrence of dominance by a few species along the entire productivity range, instead of at high productivity only, may partly be explained by variation in maximum productivity levels for different limiting nutrients.

Besides productivity, differences in potential species pool sizes may explain variation in species richness in wetlands, since potential species pool sizes appear to be affected by environmental factors such as acidity, flooding, or salinity (Gough et al. 1994, Grace 1999). We evaluated whether the kind of nutrient limitation also may affect potential species pool sizes. Overall variation in species richness was not significantly different between N-limited, P (co)-limited, and K (co)-limited sites (Appendix C). Maximum richness also hardly differed between N-limited (43) and P (co)-limited (39) sites. Maximum species richness may be somewhat lower at K (co)-limited sites (32 in our study), but with 11 sites the number of observations was rather low. We conclude that the pools of European wetland species with adaptations to N- and P-limited conditions seem rather similar. Hence, it seems likely that the kind of nutrient limitation has a much smaller effect on species richness through regional species pool sizes than acidity, flooding, or salinity (cf. Grace 1999, Grace and Jutila 1999, Olde Venterink et al. 2001b).

Threatened species vs. productivity and the kind of nutrient limitation

The overall species richness–productivity pattern for threatened species (including all kinds of limitation; Fig. 3E) indicated a sort of “filled” hump-shaped pattern, which was clearly narrower than that for all vascular species (Fig. 3A). Similar patterns were observed for Canadian and British wetlands (cf. Moore et al. 1989, Wheeler and Shaw 1991). The absence of threatened species at productivity levels >500 g/m² supports the notion that nutrient enrichment and productivity increase is likely an important cause for the disappearance of the threatened species in wetlands (cf. Stanners and Bourdeau 1995).

A second difference between species richness–productivity patterns for all species and for threatened species is that ranges in richness of threatened species differed between our N-limited and P (co)-limited wetlands, whereas overall richness did not (Fig. 3, Appendix C). From the 48 threatened species in our sites,

28 were only or mostly observed at P (co)-limited sites, whereas only four species occurred primarily at N-limited sites; none of the species was specific for K (co)-limited sites (values also include threatened bryophytes; Appendix D). This indicates that many threatened species are particularly sensitive to an increase in P availability, which is supported by an earlier observed negative relationship between soil P availability and richness of threatened species (Olde Venterink et al. 2001b).

The highest richness of threatened species was found in P (co)-limited meadows of the *Junco-Molinion* community and rich fens of the *Caricion davallianae* community, making these wetland types hot spots for conservation. P (co)-limitation in these wetland types is often maintained by chemical adsorption of P in the calcium or iron-rich soils (Grootjans and Van Diggelen 1995, Wassen et al. 1996). As P availability increases (e.g., through reduced calcium or iron supply by altered groundwater flow) threatened species may be excluded by superior competitors at P-limited conditions. Furthermore, an increase in P availability may cause a shift from P (co)-limited to N-limited or K (co)-limited conditions, making adaptations to P limitation no longer beneficial. Such a shift would indeed make these species sensitive to competitive exclusion if their adaptations are accompanied by a reduced aboveground productivity.

CONCLUSIONS

This study shows that the kind of nutrient limitation may have a strong influence on the productivity level that can be attained and on species richness dependent on productivity. The kind of limitation also affected the richness–productivity patterns for threatened species. However, a high species richness does not coincide necessarily with a large number of threatened species. Conservation of many threatened European wetland plants requires low productive P (co)-limited conditions. Caution must be taken in management measures to reduce productivity, such as re-wetting and hay-making, since these measures may change the kind of nutrient limitation (Koerselman et al. 1990, Van Dur-en and Pegtel 2000, Olde Venterink et al. 2002a, b) and hence may affect species richness and the occurrence of threatened species.

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APPENDIX A

A list of data from 44 fertilization experiments from literature used in this study, as well as results of a statistical analysis of the data is available in ESA's Electronic Data Archive: *Ecological Archives* E084-053-A1.

APPENDIX B

A list of data from the 150 wetland sites used in this study and the references to previous studies is available in ESA's Electronic Data Archive: *Ecological Archives* E084-053-A2.

APPENDIX C

A table with the results of Levenes test for homogeneity of variance in species richness among N-, P-, and K-limited sites is available in ESA's Electronic Data Archive: *Ecological Archives* E084-053-A3.

APPENDIX D

A list of threatened species occurring at N-, P-, or K-limited sites is available in ESA's Electronic Data Archive: *Ecological Archives* E084-053-A4.