



Re-assessment of phosphorus availability in fens with varying contents of iron and calcium

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Abstract

Aim To further unravel P availability in mineral-rich fens, and test whether high Fe in the soil would lead to low P availability to the vegetation.

Methods Mesotrophic fens were selected over gradients in Ca and Fe in central Sweden and the Netherlands, to study characteristics of vegetation, pore water and peat soil, including inorganic and organic forms of P, Fe and Al.

Results Soil Fe was more important than region or soil Ca, and P availability to the vegetation increased from

Fe-poor to Fe-rich fens. Contrary to expectations, precipitation of iron phosphates played a minor role in Fe-rich fens. Fe-rich fens were P-rich for three reasons: (1) high P sorption capacity, (2) relatively weak sorption to Fe-OM complexes and (3) high amounts of sorbed organic P, which probably consists of labile P. Also, nonmycorrhizal wetland plants probably especially take up weakly sorbed (organic) P. However, high P did not lead to high biomass or low plant diversity. Fe-rich fens were limited by other nutrients, and high P may help protect the vegetation against Fe-toxicity.

Highlights

- This study provides further evidence that Fe-rich fens are not P-poor but P-rich
- Fe-rich fens have high total P, but especially a lot of weakly sorbed P_i and P_o
- High P in Fe-rich fens does not lead to high biomass, but may reduce Fe-toxicity
- Ca-rich fens are P-poor, mainly due to low Fe and low P-sorption capacity

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Conclusions Fe-poor fens are P-poor, irrespective of Ca, and Fe-rich fens P-rich even under mesotrophic conditions. However, high P itself does not endanger Fe-rich fens.

Keywords Mineral-rich fens · Plant diversity · Nutrients · Humic Fe-Al complexes · Central Sweden · The Netherlands

Introduction

Mineral-rich fens are important habitats for biodiversity. They are rich in spectacular and strictly restricted plant species (European Union 2013), and home to the EU-habitat directive species such as *Hamatocaulis vernicosus* and *Liparis loeselii*. Mineral-rich fens belong to protected EU-habitat types such as Transition mires (H7140), Alkaline fens (H7230) and *Molinia* meadows on calcareous, peaty or clayey-silt laden soil (H6410), but they have undergone a serious decline in Europe. Apart from habitat destruction and drainage, mineral-rich fens are threatened by eutrophication and acidification (Lamers et al. 2015). They are often fed by groundwater, and can be Ca-rich and/or Fe-rich, depending on geological substrate, hydrology and water chemistry.

Nutrient availability in mineral-rich fens has been studied rather extensively in the past (e.g., Boyer and Wheeler 1989; Verhoeven et al. 1990; Snowden and Wheeler 1993, 1995; Wassen et al. 2005; Kooijman and Paulissen 2006). However, recent studies have provided controversial insights, especially related to availability of P in Fe-rich fens (Zak et al. 2008; Aggenbach et al. 2013; Pawlikowski et al. 2013; Cusell et al. 2014; van der Grift et al. 2016; Emsens et al. 2017).

Iron-rich soils are generally seen as P-limited, due to proposed stable P binding at Fe compounds (Walker and Syers 1976; Hamad et al. 1992). In aquatic ecosystems, P-poor water and high plant diversity are associated with high Fe:P ratios in water and soil (e.g., Geurts et al. 2008). The principle of P capture by Fe is even used in phosphate removal from polluted surface water or agricultural runoff (Thistleton et al. 2001; Zou et al. 2018). In Fe-rich fens, sorption of P to, or precipitation with Fe may thus be an important mechanism to reduce P-availability in soil pore water (Zak et al. 2004). When anoxic, Fe-rich groundwater is aerated, precipitation of iron hydroxyphosphates may even precede formation of

iron (hydr)oxides as long as dissolved orthophosphate is present (van der Grift et al. 2016).

However, in semi-terrestrial Fe-rich peat soils, P availability may not be low at all. Recent studies showed that P in vegetation and/or soil increased with Fe content of the peat soil instead of decreased, which would hamper restoration of formerly drained Fe-rich fens (Aggenbach et al. 2013; Pawlikowski et al. 2013; Emsens et al. 2017). In their studies, foliar N:P ratios dropped below the critical level of 14.5 g g^{-1} , which do not point to P limitation, but to excess of P (Olde Venterink et al. 2003). High P availability in Fe-rich fens may be caused by permanently high water levels, which leads to anoxic conditions, reduction of Fe(III) and mobilization of Fe-bound P (Patrick and Khalid 1974; Lamers et al. 2012). However, high plant P contents and foliar N:P ratios below 10 g g^{-1} were found in Fe-rich soils even under well-drained conditions (Emsens et al. 2017), so other factors play a role as well. In Fe-rich fens, P availability to the vegetation could also increase if a large part of the P is sorbed to complexes of Fe and organic matter (OM), rather than to Fe (hydr)oxides (Kooijman et al. 2009; Gerke 2010; van der Grift et al. 2016). Sorption of P to Fe-OM complexes provides a weaker form of binding, but is often ignored in studies about P-availability (Gerke 2010, 2015).

Even though P availability to the vegetation may be higher than expected in Fe-rich fens, it is unclear whether such a high P availability in Fe-rich fens actually leads to higher biomass production and light limitation to smaller fen species (Aggenbach et al. 2013). Emsens et al. (2017) showed that the total amount of P in the aboveground vegetation clearly increased with Fe content of the soil, but aboveground biomass itself seemed less affected. In addition, Cusell et al. (2014) showed that aboveground biomass production in Fe-rich fens did not increase when fertilized with P, while Pawlikowski et al. (2013) did not find differences in aboveground biomass between Ca-rich and Fe-rich fens.

For Ca-rich fens, views on P-availability to the vegetation are less ambiguous. Ca-rich fens are generally regarded as P limited (e.g., Boyer and Wheeler 1989; Wassen et al. 2005; Pawlikowski et al. 2013; Cusell et al. 2014; Kooijman et al. 2016), and eutrophication with P is considered to be a major threat to plant diversity (Kooijman and Paulissen 2006; Lamers et al. 2015). However, the mechanisms for low P availability in Ca-rich fens are not always clear. Calcium phosphates becomes coprecipitated with calcium carbonates in fens

with Ca-rich groundwater (Boyer and Wheeler 1989), which are sparingly soluble around pH 7 (Lindsay and Moreno 1966; Hinsinger 2001). However, in many Ca-rich fens, Ca-concentrations are often too low for calcite precipitation. In the view of Emsens et al. (2017), these fens may be limited by P due to low Fe levels and low P-sorption capacity, rather than high Ca contents.

The goal of the present study was to further unravel the regulation of P availability to the vegetation in different mineral-rich fens. We studied 25 mesotrophic and undrained mineral-rich fens over gradients from 0.2 to 8.1 mol kg⁻¹ Ca in the soil and from 0.02 to 2.2 mol kg⁻¹ Fe. In order to test whether relationships between P, Fe and Ca differed between regions, 12 fens were selected in undisturbed areas in central Sweden, and 13 in areas with high human impact in the Netherlands. In each fen, we studied plant species composition, aboveground biomass, pore water and peat soil chemistry. We also measured different soil fractions of P, Fe and Al, such as total P, inorganic P, organic P, sorbed P and exchangeable P, and total, inorganic and organic amorphous Fe and Al. We included organic fractions, because organic P may be a major source of P to the vegetation in these ecosystems (Pérez Corona et al. 1996; Turner et al. 2007; Cheesman et al. 2014; Güsewell 2017), and organic Fe and Al are part of humic Fe-OM and Al-OM complexes, which show weaker P sorption than Fe and Al (hydr)oxides (Gerke 2010). The research questions were (1): Does P availability to the vegetation differ with respect to Fe and/or Ca content of the peat soil, and between regions? (2) Does higher P availability to the vegetation in particular fen types lead to higher plant biomass and lower species richness?

Methods

Field survey

Vegetation, soil and pore water samples were collected at the end of August and beginning of September in 13 fens with varying contents of iron and calcium in the Netherlands and 12 in central Sweden (Table 1). Selection of the sites was based on the presence of bryophytes such as *Calliergon giganteum* (Schimp.) Kindb., *Scorpidium scorpioides* (Hedw.) Limpr., *S. cossonii* (Schimp.) Hedenäs and *Hamatocaulis vernicosus* (Mitt.) Hedenäs, which are characteristic for mesotrophic fens, and occur over a range of Ca-rich to Fe-rich habitats (Mettrop et al. 2018). In central Sweden, all fens

were characterized by groundwater seepage areas, but Ca-rich fens were found in areas with limestone and marl parent materials, while Fe-rich fens were found in areas with granitic glacial deposits. In the Netherlands, most Fe-rich fens also occurred in groundwater seepage areas, although two were regularly flooded with Fe-rich river water. However, many Dutch sampling localities were located in areas without groundwater seepage. Instead, these fens were fed by nutrient-poor and base-rich surface water.

For each of the 25 sites, species composition and cover percentages of vascular plants and bryophytes were recorded in a 10 m² plot, with nomenclature according to Van Tooren and Sparrius (2007) for the first, and van der Meijden (2005) for the latter. In each plot, three subplots were randomly selected. In each subplot, height of the water level was measured relatively to the soil surface just beneath the living moss layer, except in two Dutch Fe-rich fens. In each subplot, living aboveground biomass of vascular plants was harvested in 25 × 25 cm squares for further analysis. Pore water samples were collected from the upper 10 cm of the soil with Rhizon SMS soil moisture samplers with pore size of 0.45 μm, connected to vacuumed syringes of 50 mL. In addition, peat soil samples were collected from the upper 10 cm of the peat soil, just below the living moss layer. Samples for bulk density were collected with a steel corer with a 100 ml volume. All samples were collected in airtight plastic bags to avoid oxygen exposure, and stored at 4 °C until further analysis.

Chemical composition

Pore water pH, electrical conductivity (EC) and alkalinity were measured on the day of sampling with standard electrodes and by titration down to pH 4.2 by using 0.01 mol L⁻¹ HCl. Subsamples were acidified with 1% HNO₃ to prevent metal precipitation. Concentrations of o-PO₄³⁻, NO₃⁻, NH₄⁺, SO₄²⁻, Cl⁻ and dissolved organic matter (DOC) were measured in the laboratory with an Skalar auto Analyzer (Westerman 1990). Unfortunately, NH₄⁺ and NO₃⁻ concentrations could not be measured in two of the Dutch Fe-rich fens. Also, in one of the subsamples of one of the Ca-rich fens in Sweden, NO₃⁻ concentrations were unrealistically high (> 250 μmol L⁻¹), and mean values for NO₃⁻ in this site were based on the other two subsamples. Total concentrations of P, Ca²⁺, Fe²⁺, S²⁻, Mg²⁺, Al³⁺, Na⁺, K⁺, Zn²⁺ and Mn³⁺ were measured for all subsamples with Perkin

Table 1 Sampling localities of mineral-rich fens with different total Fe and Ca content in the peat soil (0–10 cm) in the Netherlands (NL) and central Sweden (S)

Site	Region	Coordinates	Soil Fe mmol m ⁻²	Soil Ca mmol m ⁻²	Log Fe	Log Ca
De Haeck	NL	52 08'59 N; 04 50'36 E	91	1199	1.95	3.08
Stobbenribben	NL	52 47'09 N; 05 59'03 E	102	2213	2.00	3.35
Kiersche Wiede	NL	52 41'48 N; 06 07'57 E	166	1928	2.22	3.28
Blauwe Hel	NL	52 00'48 N; 05 34'16 E	308	2135	2.49	3.33
Kikkerlanden	NL	52 39'45 N; 06 02'27 E	529	2526	2.72	3.40
Geleenbeekdal	NL	50 55'34 N; 05 54'03 E	609	3487	2.79	3.54
Veldweg	NL	52 41'29 N; 06 06'45 E	748	4865	2.87	3.69
Tienhoven South	NL	52 10'31 N; 05 59'01 E	750	1508	2.87	3.18
Tienhoven North	NL	52 10'31 N; 05 59'01 E	1085	1978	3.04	3.30
Bennekomse Meent	NL	52 00'22 N; 05 35'37 E	1139	3315	3.06	3.52
Veerslootlanden	NL	52 37'09 N; 06 08'15 E	3511	4528	3.54	3.66
Meppelerdieplanden	NL	52 40'05 N; 06 07'37 E	3580	2102	3.55	3.32
Meppeler Diep	NL	52 41'00 N; 06 08'51 E	8044	2992	3.91	3.48
Gulåstjärnen 2	S	63 29'17 N; 14 53'48 E	76	203,439	1.85	5.31
Gulåstjärnen 1	S	63 29'17 N; 14 53'48 E	167	124,325	2.22	5.09
Gulåstjärnen lake 1	S	63 29'17 N; 14 53'48 E	408	5497	2.62	3.74
Gulåstjärnen lake 2	S	63 29'17 N; 14 53'48 E	500	8425	2.70	3.93
Stormyran 3	S	63 13'15 N; 16 09'22 E	1503	1773	3.18	3.25
Stormyran 2	S	63 13'15 N; 16 09'22 E	1719	2513	3.23	3.40
Storflon 1	S	63 13'33 N; 16 00'45 E	4483	1338	3.65	3.13
Stormyran 1	S	63 13'15 N; 16 09'22 E	6427	2983	3.81	3.47
Flärkarna 1	S	63 04'01 N; 16 10'43 E	7652	4585	3.88	3.66
Flärkarna 2	S	63 04'01 N; 16 10'43 E	14,031	4063	4.15	3.61
Storflon 2	S	63 13'33 N; 16 00'45 E	15,346	2323	4.19	3.37
Kjällmyran	S	63 24'10 N; 14 34'07 E	18,947	3858	4.28	3.59

Log Fe and log Ca in the soil are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil in mmol m⁻². For each site, total Fe and Ca contents are average values, based on three replicate samples

Elmer Inductively Coupled Plasma - Optical Emission Spectrometry (ICP-OES) spectroscopy (Westerman 1990). It is possible that Fe²⁺ concentrations in pore water samples of Fe-rich fens have been overestimated to some extent, due to oxidation of this element during the sampling process, and re-dissolution after the samples had been treated with 1% HNO₃. Dissolved organic P (DOP) was calculated as the difference between total dissolved P and o-PO₄. In one of the subsamples of one of the Dutch Ca-rich fens, total P, PO₄³⁻ and DOP concentrations were exceptionally high (> 10 μmol L⁻¹), and mean values for P in pore water in this site were based on the other two subsamples.

Vegetation samples were weighed after drying at 70 °C until constant weight, and ground. Total C and N contents were measured in dried vegetation samples,

using a Elementar CHNS analyzer (Westerman 1990). In addition, dry plant material was digested for 50 min in a Perkin Elmer microwave with HNO₃ (65%) and HCl (37%), after which total P, Ca, Fe, S, Mg, Al and K contents in diluted digestates were measured by ICP (Westerman 1990). For plant material, N, P and K contents were expressed in g rather than mol, because critical nutrient ratios, which are used as indicators of which type of nutrient is limiting plant growth, are generally given in g g⁻¹ (Olde Venterink et al. 2003). Critical levels are 14.5 g g⁻¹ for N:P ratios, 2.1 g g⁻¹ for N:K ratios and 3.4 mg g⁻¹ for K:P ratios.

Dry weights and gravimetric moisture contents of the fresh peat soil samples were determined by drying at 70 °C until constant weight. Total organic matter (OM) contents were estimated for all subsamples by loss-on-ignition at

550 °C. Total C and N contents were measured in dried peat soil samples with a CHNS analyzer. In addition, total P, Ca, Fe, S, Mg, Al and K contents were measured with microwave destruction (Westerman 1990). Samples of dry soil were digested for 50 min in a microwave with 4.0 mL HNO₃ (65%) and 1.0 mL HCl (37%).

In one of the Dutch Ca-rich and one of the Dutch Fe-rich fens, one of the three subsample showed 3–8 times higher amounts of amorphous than total Fe, which is impossible. These subsamples were discarded for all parameters, and mean values for these sites based on the other two subsamples.

Fractionation of P, Fe and Al

Different mobile P, Fe and Al fractions were determined using established chemical extraction procedures. It must be noted that the interpretation of results must be undertaken with caution since both the extraction procedure as well as used chemicals causes some limitations (Kooijman et al. 1998, 2009). The P, Fe and Al fractions were measured on lyophilized peat soil samples in order to restrict redox sensitive reactions and to keep soil moisture contents equal. For the 75 subsamples of the 25 sites, we measured total P, inorganic P, organic P and sorbed P. Total P content (after heating at 500 °C for 4 h) and inorganic P content (not heated) were extracted with 0.5 M H₂SO₄, and measured colorimetrically (Westerman 1990). With this method, total P was on average 85% of the total P measured on dry soil with microwave destruction, but the two values highly correlated ($R^2 = 0.97$). Organic P was calculated as the difference between total and inorganic P. Sorbed P was measured with 0.073 M NH₄-oxalate/0.05 M oxalic acid extraction at pH 3.0 and subsequent element analysis by ICP (Schwertmann 1964).

Total P consisted of inorganic and organic P, which each consisted of solid or stable and sorbed P fractions. These fractions could not be measured directly, but minimum and maximum estimates could be calculated for solid inorganic P such as calcium or iron phosphates, sorbed inorganic P, stable organic P and sorbed organic P, based on the overlap and differences between the measured amounts of inorganic, organic and sorbed P (Kooijman et al. 2009). In many fens, sorbed P was larger than inorganic P, which means that at least part of the sorbed P was organic. In these fens, the difference between sorbed and inorganic P thus represented a minimum estimate of sorbed organic P. The amount of

sorbed P itself was considered as a maximum estimate of sorbed organic P. In three Ca-rich fens, however, sorbed P was smaller than inorganic P, and larger than organic P. In that case, the minimum estimate of sorbed organic P was zero, and the maximum estimate the amount of organic P itself. When the minimum and maximum estimates of sorbed organic P were known, it was possible to calculate maximum and minimum estimates for sorbed inorganic P, by subtracting the values for sorbed organic P from the total amount of sorbed P. When minimum and maximum estimates of sorbed organic and inorganic P were known, it was also possible to calculate estimates for stable organic P and solid inorganic P, by subtracting the values for the sorbed fractions from the total amounts of organic or inorganic P.

Exchangeable and EDTA-extractable P were measured with sequential extractions according to Golterman (1996) on the three subsamples of 9 sites in the Netherlands, and 12 sites in central Sweden. For this analysis, the Dutch sites Blauwe Hel, Geleenbeekdal, Tienhoven North and Bennekomse Meent were not included. For exchangeable P, freeze dried and chopped samples were shaken in 1 M NH₄Cl. After this, Fe-bound P was measured in extracts with 0.05 M Ca-EDTA. After this, Ca-bound P, consisting of weakly sorbed inorganic and organic P to Ca compounds was measured in extracts with 0.1 M Na₂-EDTA.

Total amorphous Fe and Al were measured for all 75 subsamples of all 25 sites with the oxalate extractions for sorbed P described above. As already mentioned, selective extractions give only a rough indication of different forms. Also, even though we tried to restrict oxidation by using lyophilized soil samples, the high amounts of Fe(III) measured in Fe-rich fens could to some extent have originated from Fe(II) compounds. We also analyzed organic Fe and Al, which are part of complexes with Fe, Al and organic matter (OM), and lead to weaker P sorption than to Fe and Al oxides (Kooijman et al. 2009; Gerke 2010). Organic Fe and Al were measured according to McKeague et al. (1971) in 0.1 M Na₄P₂O₇ extracts with the Auto Analyzer. Inorganic amorphous Fe + Al, present in amorphous oxides and phosphates, were calculated as the difference between total amorphous and organic Fe + Al. Part of the organic Fe + Al may consist of small inorganic Fe + Al particles, especially in Fe-rich soils with mobilization and precipitation of Fe (Jeanroy and Guillet 1981). These particles probably mostly consist of fine colloids

of iron hydroxides, associated with some organic matter, which are important to P binding (Bol et al. 2016). In any case, in Fe-rich dunes, the amount of plant-available P positively correlated with the fraction of so-called organic, pyrophosphate-extractable Fe, and negatively with inorganic Fe (Kooijman et al. 2009).

Statistical analysis

The 25 vegetation relevés were clustered with Twinspan (Hill 1979), with standard options. The statistical analysis of all other parameters was based on mean values for each of the 25 sites, or 21 sites in the case of exchangeable, Ca-EDTA and Na-EDTA extractable P. For each parameter except number of plant species, mean values were based on the three subsamples measured in each site. Potential effects of Ca and Fe content of the soil, as well as region, were tested with stepwise multiple linear regressions, with log Fe, log Ca and region as explanatory variables (Cody and Smith 1987). Log Fe and log Ca in the soil were both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil, given in mmol m^{-2} . Univariate relationships between individual parameters were further tested with Pearson correlation tests. Most parameters showed linear relationships with soil Fe and/or Ca, but for total and inorganic amorphous Fe + Al, second order relationships were more appropriate.

Results

Plant diversity and biomass

We encountered 46 bryophyte and 151 vascular plant species in the vegetation in total. In the first Twinspan division, fens in the Netherlands were separated from those in central Sweden (Table 2). This distinction was primarily based on plant species with different distribution patterns. In the Netherlands, temperate species prevailed, such as the EU-habitat directive species *Liparis loeselii*, which does not occur in Sweden at all, and the bryophyte *Calliergonella cuspidate*, which only occurs in the southern part. In central Sweden, boreal species were more common, such as *Trichophorum alpinum* and *Paludella squarrosa*, which are absent from the Netherlands. In both regions, the fens were separated into relatively Fe-poor and Fe-rich ones.

Aboveground vascular plant biomass also differed between the Netherlands and central Sweden, with higher values for the first, possibly due to the more temperate climate (Table 3, Fig. 1). However, plant species richness did not differ between regions. The total number of plant species ranged around 27 in both the Netherlands and central Sweden, although the number of bryophytes was significantly higher in the latter. Total plant species number did also not change with Fe or Ca in the soil, although the number of herb species was significantly lower in Ca-rich fens. Even though cover of the herb layer was significantly lower in Ca-rich fens, aboveground vascular plant biomass did also not differ between Fe-poor and Fe-rich fens, or Ca-poor and Ca-rich fens.

Vascular plant nutrients

Plant nutrient contents strongly correlated with soil Fe, but did not differ between regions or with Ca content of the soil (Table 4). Plant N, P and K contents were all significantly higher in Fe-rich than in Fe-poor fens. Iron content of the soil especially correlated with plant P contents, which more than quadrupled from Fe-poor to Fe-rich fens (Fig. 2). Vascular plant N:P ratios also clearly correlated with Fe content of the soil. Values decreased from approximately 25 g g^{-1} in Fe-poor fens, which point to P limitation, to 10 g g^{-1} in Fe-rich fens, which indicate that P is not all a limiting factor for plant growth. The plants showed balanced N:P ratios of 15 g g^{-1} around log Fe values of 3.7, or total Fe contents of 5000 mmol m^{-2} .

However, although plant P contents clearly increased with soil Fe, the total amount of P in aboveground vascular plant biomass did not differ between Fe-poor and Fe-rich fens, probably because vascular plant biomass was not affected by soil Fe. For the entire dataset, the correlation between soil Fe and total plant P showed a R^2 value of 0.12. In the stepwise multiple regression for total plant P, log Fe came out after region, and showed significant additional effects only in central Sweden.

Pore water characteristics

At the time of sampling, the water table did not differ with soil Ca or Fe content, or between regions, and was close to the surface in all fens (Table 5). The pH of the pore water increased with Ca content in the soil, with values ranging from 6.2 in Ca-poor fens to 7.2 in Ca-

Table 2 Twinspan clustering of mineral-rich fens with different soil Fe and Ca content in the Netherlands and central Sweden. Eigenvalues were 0.567 at the first division, 0.464 at the second division, and 0.420 at the third division. In the first division, the two regions were completely separated. In the second and third

divisions, for both countries, Fe-rich fens were separated from Fe-poor fens. Only species with frequency of 50% in at least one of the groups are listed

Twinspan group	1	2	3	4
Region	NL	NL	S	S
Soil Fe-content (mol m ⁻²)	0.3	2.1	1.3	12.5
Number of sites	n=4	n=9	n=7	n=5
Vascular plants				
<i>Liparis loeselii</i>	75	-	-	-
<i>Thelypteris palustris</i>	75	-	-	-
<i>Erica tetralix</i>	50	-	-	-
<i>Eupatorium cannabinum</i>	50	-	-	-
<i>Galium uliginosus</i>	50	-	-	-
<i>Lysimachia thyrsiflora</i>	50	-	-	-
<i>Myrica gale</i>	50	-	-	-
<i>Typha angustifolia</i>	50	-	-	-
<i>Lythrum salicaria</i>	100	56	-	-
<i>Cirsium palustre</i>	100	22	-	-
<i>Hydrocotyle vulgaris</i>	75	78	-	-
<i>Mentha aquatica</i>	75	67	-	-
<i>Lysimachia vulgaris</i>	75	44	-	-
<i>Peucedanum palustre</i>	75	33	-	-
<i>Viola palustris</i>	75	11	-	-
<i>Juncus subnodulosus</i>	50	44	-	-
<i>Carex diandra</i>	50	22	-	-
<i>Alnus glutinosa</i>	50	11	-	-
<i>Calamagrostis canescens</i>	50	11	-	-
<i>Agrostis canina</i>	25	67	-	-
<i>Juncus articulatus</i>	-	78	-	-
<i>Ranunculus flammula</i>	-	56	-	-
<i>Drosera rotundifolia</i>	75	-	43	-
<i>Betula pubescens</i>	50	-	14	-
<i>Galium palustre</i>	-	67	-	20
<i>Pedicularis palustris</i>	50	67	57	60
<i>Carex lasiocarpa</i>	50	44	100	60
<i>Potentilla erecta</i>	50	11	14	20
<i>Equisetum palustre</i>	25	22	29	60
<i>Menyanthes trifoliata</i>	25	89	43	100
<i>Equisetum fluviatile</i>	25	67	43	80
<i>Phragmites australis</i>	100	67	14	-
<i>Utricularia minor</i>	50	22	14	-
<i>Molinia caerulea</i>	50	11	43	-
<i>Potentilla palustre</i>	75	78	-	20
<i>Salix cinerea</i>	75	11	-	20
<i>Carex panicea</i>	-	44	100	-
<i>Carex nigra</i>	-	56	57	20
<i>Carex rostrata</i>	-	56	86	100
<i>Betula pendula</i>	-	-	14	60
<i>Carex chordorrhiza</i>	-	-	29	80
<i>Carex limosa</i>	-	-	29	60
<i>Oxycoccus palustris</i>	-	-	43	80
<i>Dactylorhiza incarnata</i>	-	-	57	40
<i>Salix myrsinites</i>	-	-	57	20
<i>Trichophorum alpinum</i>	-	-	71	80
<i>Rumex acetosa</i>	-	-	-	60
Bryophytes				
<i>Sphagnum subnitens</i>	50	-	-	-
<i>Calliergonella cuspidata</i>	100	89	-	-
<i>Sphagnum contortum</i>	50	-	43	-
<i>Bryum pseudotriquetrum</i>	100	22	71	60
<i>Campyllum stellatum</i>	100	22	100	40
<i>Calliergon giganteum</i>	50	44	14	80
<i>Scorpidium cossonii</i>	25	33	86	60
<i>Fissidens adiantoides</i>	75	11	14	-
<i>Scorpidium scorpioides</i>	75	22	86	-
<i>Hamatocaulis vernicosus</i>	25	44	-	100
<i>Sphagnum teres</i>	50	-	14	60
<i>Straminergon stramineum</i>	25	-	-	60
<i>Aneura pinguis</i>	25	-	71	20
<i>Paludella squarrosa</i>	-	-	14	80
<i>Tomentypnum nitens</i>	-	-	14	80
<i>Sphagnum warnstorfia</i>	-	-	29	60
<i>Drepanocladus trifarium</i>	-	-	57	-
<i>Helodium blandowii</i>	-	-	-	60

Table 3 Stepwise multiple linear regression of vegetation characteristics, with Fe and Ca content of the soil and region as explanatory variables. The analysis is based on 25 samples from the Netherlands and central Sweden, all based on three subreplicates

Variable	R ² log Fe soil	R ² log Ca soil	R ² region	Total R ²
Vascular plant biomass	0.02	0.03	0.30	0.35**
Herb cover	–	0.36	–	0.36**
Moss cover	0.06	0.02	0.10	0.18 ^{ns}
Total species number	–	–	0.10	0.10 ^{ns}
Number of herb species	–	0.37	–	0.37**
Number of moss species	0.03	0.03	0.19	0.25*

Log Fe and log Ca in the soil are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil in mmol m^{-2} . Ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Variables explaining more than 17% of the variance in a particular parameter are given in bold

rich fens, but did not differ between regions or with soil Fe. Alkalinity was not correlated with region, soil Fe or Ca content, but ranged around 2.2 mol L^{-1} in all fens. Electrical conductivity however clearly differed between regions, with average values of $209 \mu\text{S cm}^{-1}$ in

central Sweden, and $374 \mu\text{S cm}^{-1}$ in the Netherlands. This was associated with higher Na^+ , Cl^- , SO_4^{2-} and DOC concentrations in the Netherlands.

At the time of sampling, pore water Ca^{2+} concentrations were also lower in the Netherlands, with average

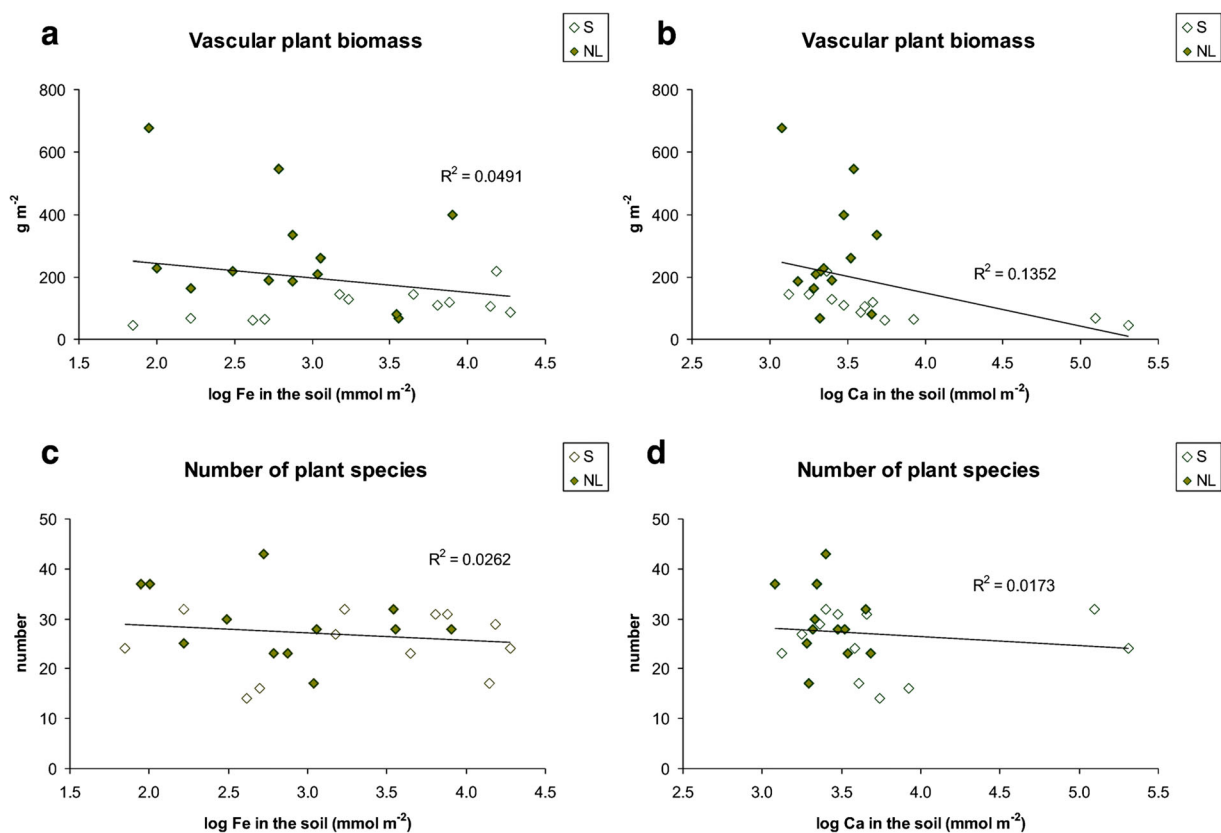


Fig. 1 Total number of plant species and vascular plant biomass in mineral-rich fens in the Netherlands and central Sweden in relation to the gradients in Fe and Ca in the soil. Log Fe and log Ca are both based on the amounts of Fe and Ca in the upper 10 cm of the peat soil, expressed in mmol m^{-2} . A = vascular plant

biomass in relation to soil Fe; B = vascular plant biomass in relation to soil Ca; C = number of plant species in relation to soil Fe; D = number of plant species in relation to soil Ca. None of the correlations was significant ($p < 0.05$)

Table 4 Stepwise multiple linear regression of plant nutrients, with Fe and Ca content of the soil and region as explanatory variables. The analysis is based on 25 samples from the Netherlands and central Sweden, all based on three subreplicates

Variable	R ² log Fe soil	R ² log Ca soil	R ² region	Total R ²
Plant N-content (mg g ⁻¹)	0.22	0.12	0.08	0.41*
Plant P-content (mg g ⁻¹)	0.36	0.04	0.02	0.43**
Plant K-content (mg g ⁻¹)	0.25	–	–	0.25*
Plant Fe-content (g g ⁻¹)	–	0.09	0.03	0.13 ^{ns}
Total plant P (g m ⁻²)	0.24	–	0.15	0.40**
Total plant N (g m ⁻²)	0.04	–	0.36	0.40**
Total plant K (g m ⁻²)	–	0.15	0.06	0.21 ^{ns}
Total plant Fe (g m ⁻²)	–	0.10	–	0.10 ^{ns}
Plant N:P ratio (g g ⁻¹)	0.35	0.02	0.05	0.42**
Plant N:K ratio (g g ⁻¹)	0.02	–	0.10	0.12 ^{ns}
Plant K:P ratio (g g ⁻¹)	0.05	0.03	0.07	0.09 ^{ns}
Plant P:Fe ratio (g g ⁻¹)	0.02	0.13	0.02	0.17 ^{ns}

Log Fe and log Ca in the soil are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil in mmol m⁻². Ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Variables explaining more than 17% of the variance in a particular parameter are given in bold

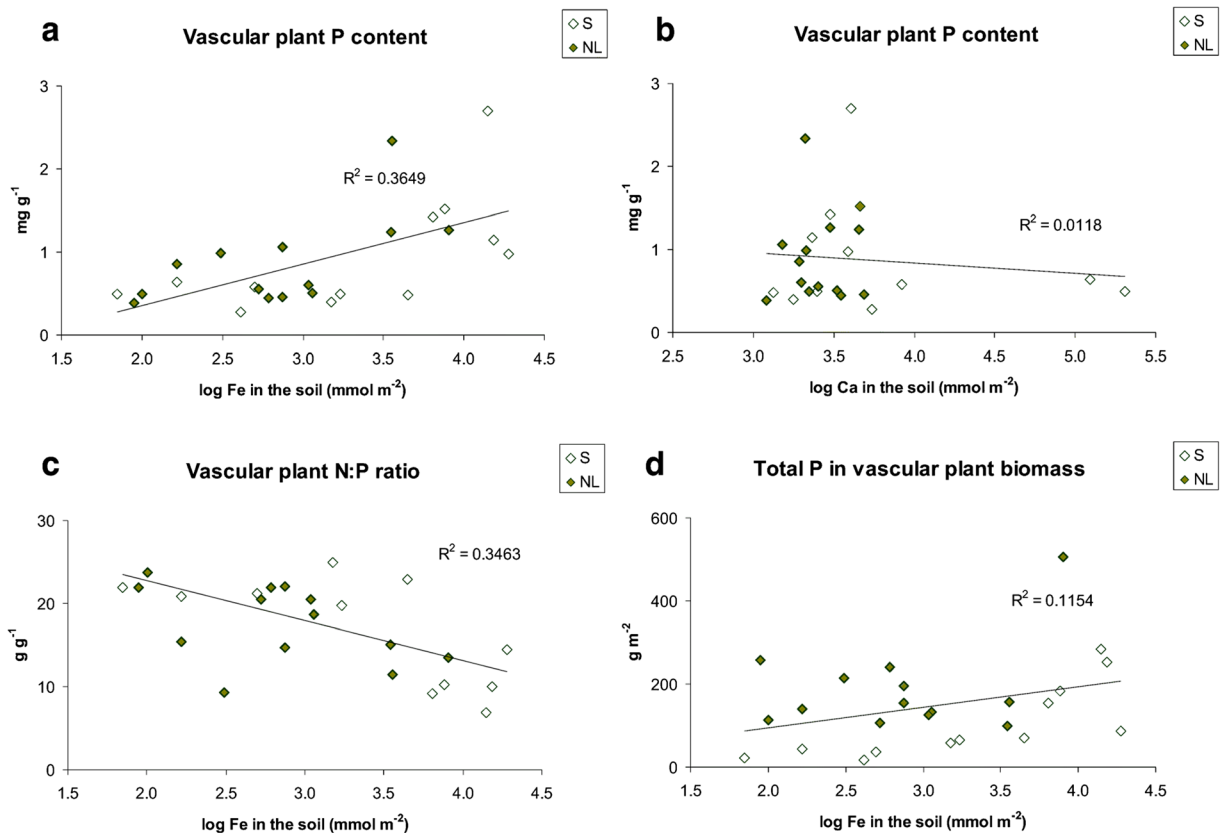


Fig. 2 Aboveground vascular plant P-content and N:P ratio in mineral-rich fens in the Netherlands and central Sweden in relation to the gradients in Fe and Ca in the soil. Log Fe and log Ca are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil, expressed in mmol m⁻². A = plant P content in relation to

soil Fe; B = plant P content in relation to soil Ca; C = plant N:P ratio in relation to soil Fe; D = plant N:P ratio in relation to soil Ca. Correlations were only significant ($p < 0.05$) for vascular plant P content and N:P ratio with log Fe

Table 5 Stepwise multiple linear regression of pore water characteristics in the peat soil, with Fe and Ca content of the soil and region as explanatory variables. The analysis is based on 25 samples from the Netherlands and central Sweden, all based on three subreplicates

Variable	R ² log Fe soil	R ² log Ca soil	R ² region	Total R ²
Water table	–	–	0.07	0.07 ^{ns}
pH	0.07	0.34	–	0.41**
Alkalinity (mmol L ⁻¹)	–	–	0.09	0.18 ^{ns}
EC (μS cm ⁻¹)	–	0.16	0.23	0.39*
Na (μmol L ⁻¹)	–	–	0.62	0.62***
Cl (μmol L ⁻¹)	0.01	0.02	0.71	0.74***
SO ₄ (μmol L ⁻¹)	0.11	0.07	0.27	0.45*
DOC (μmol L ⁻¹)	0.04	–	0.34	0.38**
Ca (μmol L ⁻¹)	–	0.10	0.17	0.27*
Mg (μmol L ⁻¹)	0.21	0.09	0.03	0.33*
K (μmol L ⁻¹)	–	–	0.07	0.07 ^{ns}
Fe (μmol L ⁻¹)	0.17	–	0.10	0.26*
Al (μmol L ⁻¹)	0.07	0.03	0.10	0.21 ^{ns}
NO ₃ (μmol L ⁻¹)	–	–	0.20	0.20*
NH ₄ (μmol L ⁻¹)	–	–	0.11	0.11 ^{ns}
PO ₄ (μmol L ⁻¹)	0.03	–	0.08	0.11 ^{ns}
DOP (μmol L ⁻¹)	0.16	–	–	0.16 ^{ns}

Log Fe and log Ca in the soil are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil in mmol m⁻². EC = Electrical conductivity. Ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Variables explaining more than 17% of the variance in a particular parameter are given in bold

values of 879 μmol L⁻¹ for central Sweden, and 1235 μmol L⁻¹ in the Netherlands, but also increased from Ca-poor to Ca-rich fens. Magnesium concentrations mainly differed with Fe in the soil, with higher values for Fe-poor fens, but K⁺ was not correlated with region or soil types. Iron concentrations mainly differed with Fe in the soil, and increased from Fe-poor to Fe-rich fens from 2 to 160 μmol L⁻¹, but Al³⁺ concentrations were not affected.

At the time of sampling, nitrate concentrations were significantly higher in central Sweden than in the Netherlands, with average values of 2.8 and 1.5 μmol L⁻¹ respectively, but did not differ with Ca or Fe content in the soil. Ammonium, phosphate and DOP concentrations did not differ between regions or along soil gradients at all.

Soil characteristics

Soil organic matter content showed significantly lower values in Ca-rich than in Ca-poor fens, due to precipitation of secondary calcium carbonates in Ca-rich fens (Table 6). However, most fens had high soil organic matter content, and average values were 79% for the Netherlands, and

73% for central Sweden. Dry weight or bulk density of the peat soil also increased in Ca-rich fens, because calcium carbonates are heavier than organic matter. However, N content and C:N ratio did not correlate with regions, soil Fe or Ca. Potassium contents of the peat soil were approximately two times higher in the Netherlands, and also increased from Fe-poor to Fe-rich soils.

Phosphorus contents in the soil, and C:P and N:P ratios, mainly correlated with Fe content. Phosphorus contents, measured by microwave destruction, increased from Fe-poor to Fe-rich fens, and C:P and N:P ratios decreased (Fig. 3). Soil C:P ratios decreased from approximately 900 g g⁻¹ in Fe-poor fens to less than 300 g g⁻¹ in Fe-rich fens. Soil N:P ratios also showed a more than threefold decrease over this gradient.

P fractions in the soil

In the selective extractions, total soil P mainly correlated with Fe content, and showed a fourfold increase from Fe-poor to Fe-rich fens (Table 7). Iron richness of the soil also affected organic P (Fig. 4). However, for inorganic P, correlations with soil Fe

Table 6 Stepwise multiple linear regression of soil characteristics (0–10 cm), with Fe and Ca content of the soil and region explanatory variables. The analysis is based on 25 samples from the Netherlands and central Sweden, all based on three subreplicates

Variable	R ² log Fe soil	R ² log Ca soil	R ² region	Total R ²
Organic matter (%)	–	0.56	–	0.56***
Dry weight (kg m ⁻²)	–	0.72	–	0.72***
Total N (g m ⁻²)	–	–	–	–
Total P (g m ⁻²)	0.28	0.12	0.08	0.47**
Total K (g m ⁻²)	0.13	0.08	0.21	0.42*
Soil C:N ratio (g g ⁻¹)	–	–	–	–
Soil C:P ratio (g g ⁻¹)	0.56	–	0.13	0.69***
Soil N:P ratio (g g ⁻¹)	0.38	–	0.11	0.49**

Log Fe and log Ca in the soil are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil in mmol m⁻². Total P is based on microwave destruction of the peat soil. Ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Variables explaining more than 17% of the variance in a particular parameter are given in bold

content were much lower, and not significant in the multiple linear regression, although they were just significant in the univariate analysis.

Sorbed, oxalate-extractable P was more strongly correlated with Fe richness of the soil than organic or inorganic P. When expressed as fraction of total P,

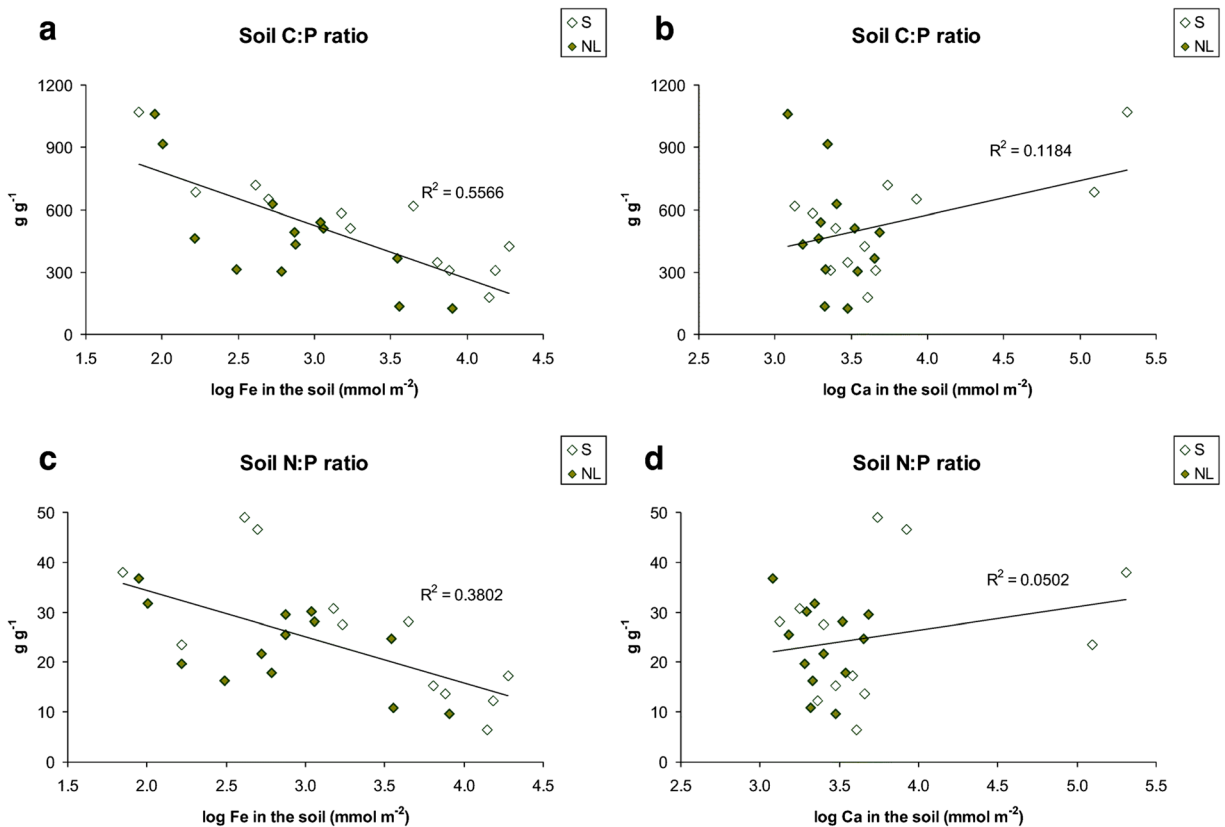


Fig. 3 Soil C:P and N:P ratio in mineral-rich fens in the Netherlands and central Sweden in relation to the gradients in Fe and Ca in the soil. Log Fe and log Ca are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil, expressed in mmol m⁻². A =

soil C:P ratio in relation to soil Fe; B = soil C:P ratio in relation to soil Ca; C = soil N:P ratio in relation to soil Fe; D = soil N:P ratio in relation to soil Ca. Correlations were significant ($p < 0.05$) for log Fe (A and C), but not for log Ca (B and D)

Table 7 Stepwise multiple linear regression of P, Fe and Al fractions in the peat soil (0–10 cm), with Fe and Ca content of the soil and region as explanatory variables. For most parameters, the analysis is based on 25 samples from the Netherlands and

central Sweden, all based on three subreplicates. However, exchangeable P, Ca-EDTA and Na-EDTA P were determined for 21 sites only

Variable	R ² log Fe soil	R ² log Ca soil	R ² region	Total R ²
Total P (mmol m ⁻²)	0.24	0.15	0.13	0.53*
Organic P (mmol m ⁻²)	0.18	0.09	0.12	0.40*
Organic P (% of total P)	0.07	0.16	–	0.23 ^{ns}
Inorganic P (mmol m ⁻²)	0.15	0.08	–	0.23 ^{ns}
Inorganic P (% of total P)	0.07	0.16	–	0.23 ^{ns}
Adsorbed P (mmol m ⁻²)	0.25	0.10	0.11	0.46*
Adsorbed P (% of total P)	0.38	0.03	0.05	0.46**
Ca-EDTA extractable P (mmol m ⁻²)	0.57	0.04	0.09	0.70***
Na-EDTA extractable P (mmol m ⁻²)	0.19	0.14	0.11	0.44*
Exchangeable P (mmol m ⁻²)	0.05	–	0.32	0.38*
Exchangeable P (% of sorbed P)	0.49	0.21	–	0.69***
Minimum estimate solid inorganic P (% Total P)	0.03	0.79	–	0.82***
Maximum estimate solid inorganic P (% Total P)	–	0.60	–	0.60***
Minimum estimate stable organic P (% Total P)	0.20	0.20	0.02	0.42*
Maximum estimate stable organic P (% Total P)	0.24	0.14	0.03	0.42*
Minimum estimate sorbed inorganic P (% Total P)	0.09	–	–	0.09 ^{ns}
Maximum estimate sorbed inorganic P (% Total P)	0.04	0.04	0.08	0.16 ^{ns}
Minimum estimate sorbed organic P (% Total P)	0.35	0.02	0.09	0.46**
Maximum estimate sorbed organic P (% Total P)	0.42	0.11	0.03	0.55***
Total Fe and Al (mol m ⁻²)	0.61	0.07	0.05	0.73***
Total amorphous Fe and Al (mol m ⁻²)	0.77	0.02	–	0.79***
Organic Fe and Al (mol m ⁻²)	0.71	0.03	0.04	0.77***
Organic Fe and Al (% of amorphous Fe and Al)	0.45	0.04	0.02	0.51***
Inorganic Fe and Al (mol m ⁻²)	0.61	–	0.05	0.66***
Inorganic Fe and Al (% of amorphous Fe and Al)	0.45	0.04	0.02	0.51***

Log Fe and log Ca in the soil are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil in mmol m⁻². Total P is based on extraction with H₂SO₄. Ns = not significant; * = p < 0.05; ** = p < 0.01; *** = p < 0.001. Variables explaining more than 17% of the variance in a particular parameter are given in bold

correlations between sorbed P and soil Fe were even higher. Sorbed P accounted for approximately 5% of total P in Fe-poor fens, but this value increased to 40% in Fe-rich fens. The increase in sorbed P with soil Fe was supported by Ca-EDTA extractable P, and to some extent by Na-EDTA extractable P, which mainly consist of sorbed P-fractions. However, exchangeable P was significantly higher for the Netherlands than for central Sweden, which may reflect the generally higher P inputs.

In many fens, sorbed P was higher than inorganic P. In fact, only three fens showed higher values for inorganic than for sorbed P. All three fens were Fe-poor, and

two of them belonged to the most Ca-rich fens. With the measurement of inorganic, organic and sorbed P, and the overlap between them, minimum and maximum estimates could be calculated for different inorganic and organic P fractions (Fig. 5). For solid inorganic P, expressed as percentage of total P, Fe in the soil was unimportant, but the amount of soil Ca explained 79% and 60% of its variance. Minimum estimates of solid inorganic P were substantially higher than zero only in the most extreme Ca-rich fens, which points to precipitation of calcium phosphates there.

Minimum and maximum estimates of stable organic P suggested that this fraction predominated in all fens.

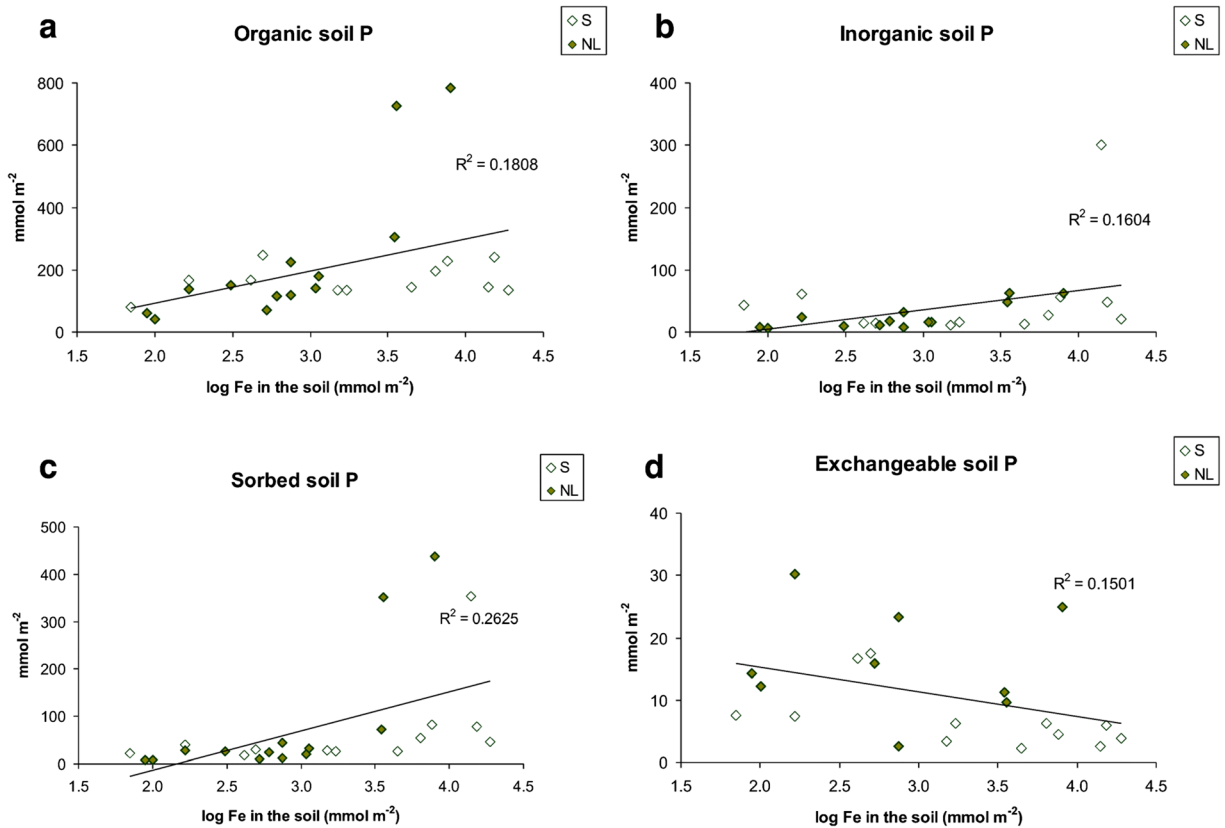


Fig. 4 Organic, inorganic, sorbed and exchangeable soil P in mineral-rich fens in the Netherlands and central Sweden in relation to Fe in the soil. Log Fe is based on the total amounts of Fe in the upper 10 cm of the peat soil, expressed in mmol m^{-2} . A = organic

P; B = inorganic P; C = oxalate-extractable sorbed P; D = NH_4Cl -extractable exchangeable P. All correlations were significant ($p < 0.05$), except for exchangeable P (D)

Both estimates correlated with Fe and Ca in the soil, and increased to some extent from Ca-poor to Ca-rich fens, but significantly decreased from Fe-poor to Fe-rich fens.

In most fens, sorbed P was higher than inorganic P, which means that at least part of the sorbed P was organic. The estimates of sorbed organic P, expressed as percentage of total P, did not differ between regions, or over gradients in soil Ca. However, both minimum and maximum estimates of sorbed organic P showed a clear increase with soil Fe. Estimates of sorbed organic P ranged between 0 and 10% of total P in Fe-poor fens, but 18–30% in Fe-rich fens. As total P also increased over this gradient, the actual increase in sorbed organic P from Fe-poor to Fe-rich fens was even higher. Also, when expressed as percentage of the amount of sorbed P, estimates of the organic P fraction increased from 0 to 21% of sorbed P in Fe-poor fens to 38–63% in Fe-rich fens.

Estimates of sorbed inorganic P, expressed as percentage of total P, did not correlate with soil Ca, Fe or

regions. However, when expressed as percentage of the amount of sorbed P, sorbed inorganic P ranged between 79 and 100% of sorbed P in Fe-poor fens, to 37–62% in Fe-rich fens.

Total, inorganic and organic Fe + Al

Total amorphous Fe + Al, which represents the total P sorption capacity, highly correlated with Fe content of the peat soil (Fig. 6). Total P sorption capacity increased at log Fe values higher than 2.7 (or $500 \text{ mmol Fe m}^{-2}$) in the topsoil. Organic and inorganic Fe + Al also increased with soil Fe. However, inorganic Fe + Al only increased when log Fe values were 3.0 (or $1000 \text{ mmol Fe m}^{-2}$) or higher. In fact, inorganic Fe + Al only substantially increased in the six most Fe-rich Swedish fens, with Fe contents of at least 4000 mmol m^{-2} . For organic Fe + Al, which consists of Fe-OM complexes, the

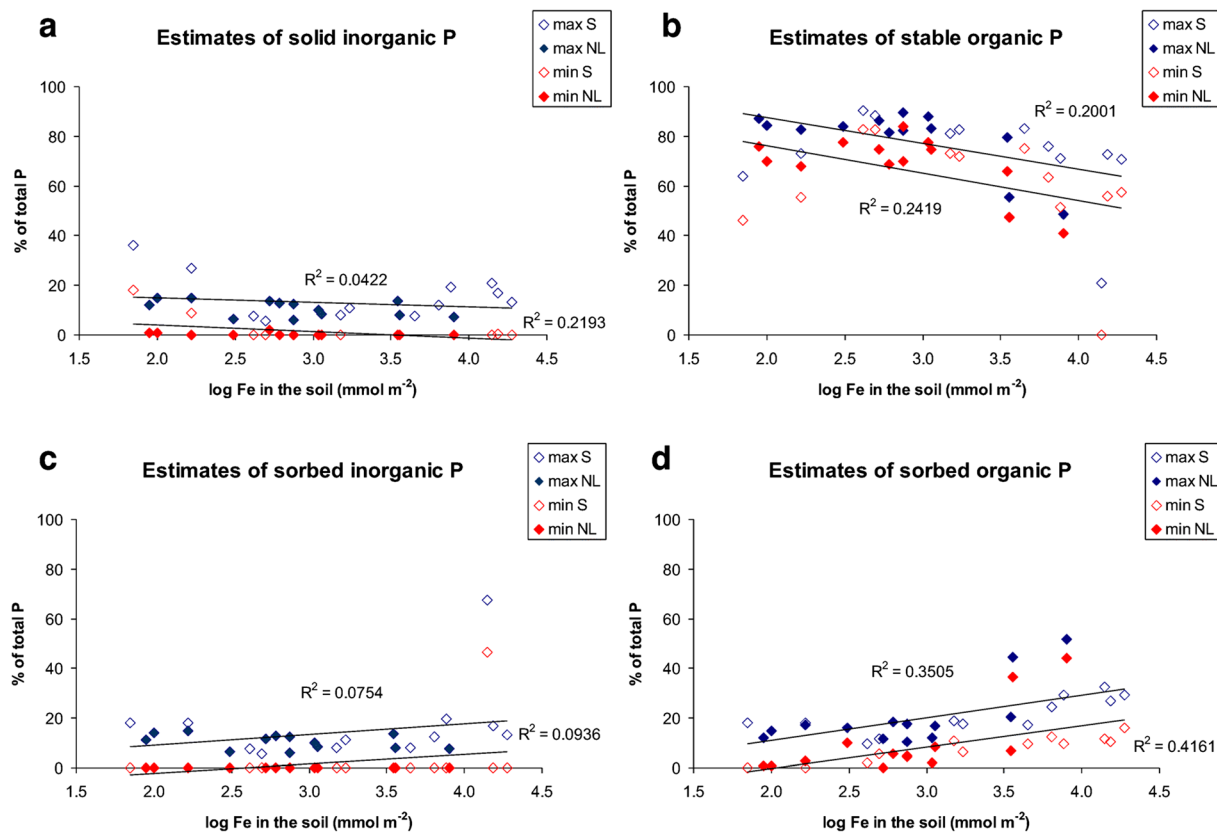


Fig. 5 Minimum and maximum estimates of different forms of inorganic and organic P in mineral-rich fens in the Netherlands and central Sweden, in relation to Fe in the soil. Log Fe is based on the total amounts of Fe in the upper 10 cm of the peat soil, expressed in

increase with soil Fe started much earlier, around 500 mmol Fe m⁻². Also, in most fens, organic Fe + Al was higher than inorganic Fe + Al, even at high soil Fe. Inorganic Fe + Al was only substantially higher than organic Fe + Al in the six most Fe-rich Swedish fens. This may imply that organic Fe + Al was more important to P sorption and plant P supply than inorganic Fe + Al.

The importance of organic Fe + Al was further supported by correlations with P-sorption and plant P-supply (Fig. 7). Plant P content and sorbed P were highly correlated, and showed R² values of 0.64 when sorbed P was expressed as log value. Sorbed P also showed high correlations with organic Fe + Al, but much lower with inorganic Fe + Al. The latter correlation was not even significant without the log-transformation of sorbed P. In addition, plant P content showed a higher correlation with organic than with inorganic Fe + Al.

mmol m⁻². A = solid inorganic P; B = stable organic P; C = sorbed inorganic P; D = sorbed organic P. Correlations were only significant ($p < 0.05$) for stable organic P (B) and sorbed organic P (D)

Discussion

Differences between the Netherlands and Central Sweden

The two regions mainly differed in vegetation characteristics and pore water composition. The fens in central Sweden typically contained plant species with a northern distribution pattern, while Dutch fens contained more temperate species. The higher vascular plant aboveground biomass in the Netherlands may have been due to the longer growing season, as the Dutch fens are located around 52° instead of 63° northern latitude. Increased nutrient supply may also play a role, as exchangeable P and total soil K were both higher in the Netherlands than in central Sweden. Also, in the Netherlands, atmospheric N-deposition is higher than in central Sweden (Erismann et al. 2015), and higher than the critical loads of 15–17 kg ha⁻¹ yr⁻¹ for *Molinion*

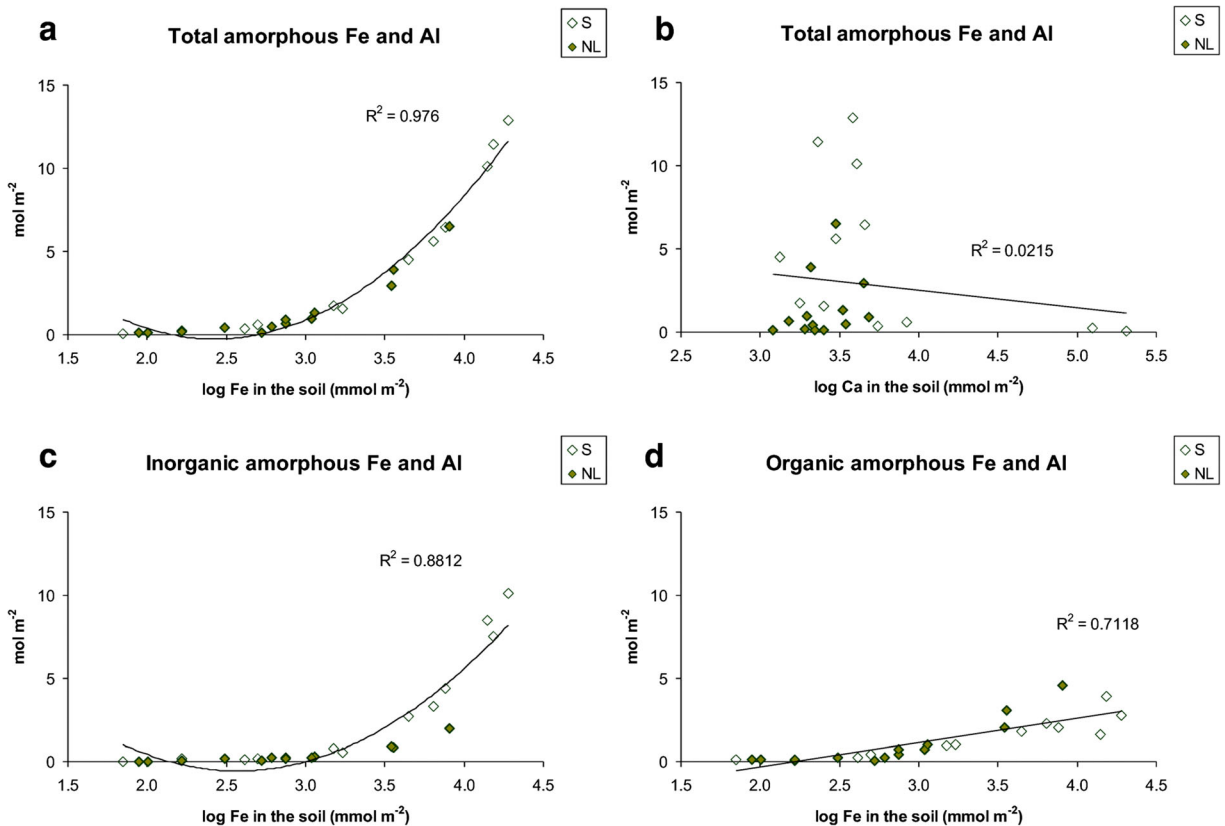


Fig. 6 Total amorphous, inorganic and organic Fe and in mineral-rich fens in the Netherlands and central Sweden in relation to the gradients in Fe and Ca in the soil. Log Fe and log Ca are both based on the total amounts of Fe and Ca in the upper 10 cm of the peat soil, expressed in mmol m^{-2} . A = total amorphous Fe + Al in

relation to soil Fe; B = total amorphous Fe + Al in relation to soil Ca; C = inorganic Fe + Al in relation to soil Fe; D = organic Fe + Al in relation to soil Fe. Correlations were significant ($p < 0.05$) for soil Fe (A, C and D), but not for soil Ca (B)

meadows, Alkaline fens or Transition mires (van Dobben and van Hinsberg 2008). Nevertheless, in both regions, the fens mostly belonged to short fens, with low biomass and high species richness, rather than tall fens (Boyer and Wheeler 1989). Plant species richness was high in both the Netherlands and central Sweden, and most plant species were characteristic for mineral-rich fens even under Fe-rich and P-rich conditions, such as the EU-habitat directive species *Hamatocaulis vernicosus*.

The two regions also differed in pore water chemistry, with higher values for EC, Na, Cl, SO₄ and DOC in the Netherlands had than in central Sweden. This may reflect the more oceanic location of the Netherlands, and/or pollution of surfacewater from the Rhine river (Cioc 2002). However, these differences in water chemistry did not affect P availability to any large extent. As already mentioned, only exchangeable P was higher in the Netherlands than central Sweden, probably due to

the generally higher input of P from agriculture in the surface water, which affects many fens there (e.g., Cusell et al. 2014).

Differences between ca-poor and ca-rich fens

Differences between Ca-poor and Ca-rich fens in vegetation, pore water and soil characteristics were smaller than expected, possibly because the gradient in soil Ca could only partly be separated from the gradient in soil Fe. However, soil organic matter content was lower in the most extreme Ca-rich fens, due to precipitation of secondary calcium carbonates (Boyer and Wheeler 1989) and the associated dilution effect. Also, these fens were the only ones in which at least part of the inorganic P consisted of solid forms, which points to co-precipitation of calcium phosphates. The fens with calcite precipitation were also characterized by low P availability and even P limitation, low herb cover and

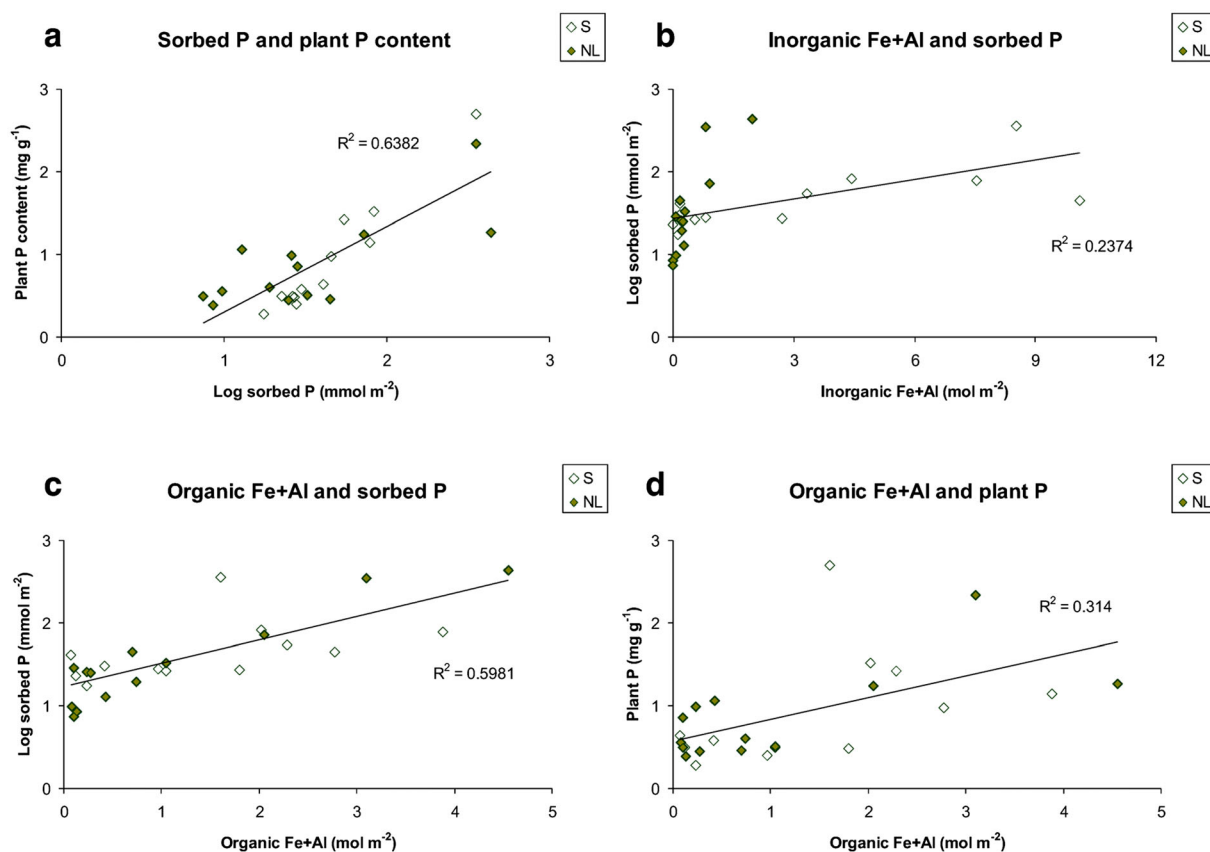


Fig. 7 Relationships between plant and soil characteristics in mineral-rich fens in the Netherlands and central Sweden. A = plant P content in relation to sorbed P in the soil; B = sorbed P in relation

to inorganic Fe + Al in the soil; C = sorbed P in relation to organic Fe + Al in the soil; D = plant P content in relation to inorganic Fe + Al in the soil. All correlations were significant ($p < 0.05$)

low number of herb species. However, in many fens, precipitation of calcium phosphate is unlikely, due to undersaturated conditions (Boyer and Wheeler 1989). For many fens with low P availability, it was more important to be Fe poor than Ca rich. In Fe-poor fens, P sorption capacity may be low, because sorption of P to organic matter is very low (Daly et al. 2001). This suggests, in accord with Emsens et al. (2017), that Fe is more important for P availability than Ca.

High P-availability in Fe-rich fens

In our study, P availability to the vegetation clearly increased from Fe-poor to Fe-rich fens. Almost all soil P fractions increased from Fe-poor to Fe-rich fens, while soil C:P ratios decreased, and vascular plant P contents more than quadrupled. The decrease in vascular plant N:P ratios from 25 to 10 g g^{-1} clearly showed that Fe-rich fens were not P limited (Olde Venterink et al. 2003),

but instead characterized by excess P. In the common view, Fe-rich soils have low P availability (Walker and Syers 1976), and high Fe concentrations reduce P loss to overlying surface water or downstream aquatic systems (Zak et al. 2004; Geurts et al. 2008; van der Grift et al. 2016). However, our findings support earlier reports that P availability within the soil may actually be higher in Fe-rich fens than in Fe-poor fens (Aggenbach et al. 2013; Pawlikowski et al. 2013; Emsens et al. 2017). High Fe levels may thus reduce orthophosphate concentrations in the water, but nevertheless increase P availability to the vegetation in the peat soil.

Inorganic, organic and sorbed P in Fe-rich fens

In Fe-rich fens, a large part of the P flowing in with groundwater and surface water is probably captured by Fe (Emsens et al. 2017), which may explain the higher amounts of total and sorbed P than in Fe-poor fens. In

theory, capture of P by Fe may lead to precipitation of Fe hydroxyphosphates (van der Grift et al. 2016). However, high amounts of inorganic P were only found in Ca-rich fens with calcite precipitation. Also, the presence of stable inorganic P could only be established with some certainty for these Ca-rich fens, which implies that precipitation of iron hydroxyphosphates in Fe-rich fens is less important than expected.

In all fens, a large part of the P was organic. We did not study the composition of organic P, but in Cheesman et al. (2014), monoesters, which mainly consist of inositol hexakiphosphates (IHP) or phytates, accounted for 62–65% of organic P in organic wetland soils. Such numbers are found in many soil types (Turner et al. 2007). Phytates are the principal storage form of P in vegetation and seeds, and consist of cyclic acids, saturated with up to six phosphate groups. With so many phosphate groups, phytates are generally more strongly bound to the soil solid phase than labile organic P (McKercher and Anderson 1989; Gerke 2015). In Ca-rich soils, phytates may even precipitate as Ca₃-IHP, which is insoluble at high pH (Prietzel et al. 2016), and may explain the high proportion of stable organic P there. In Fe-rich fens, phytates may precipitate with Fe, but especially with Al (Shang et al. 1992).

In most fens, at least part of the organic P consisted of sorbed organic P. Even though only minimum and maximum estimates could be calculated, sorbed organic P most likely increased from Fe-poor to Fe-rich fens. Sorbed organic P probably mostly consists of labile forms, as phytates are more strongly bound to the soil solid phase (McKercher and Anderson 1989; Gerke 2015). Sorbed organic P is probably an important P source for wetland plants. In terrestrial Ca-rich or Fe-rich habitats, arbuscular mycorrhizal plants predominate, because they efficiently take up inorganic calcium or iron phosphates with their mycorrhizal network (Hoeksema et al. 2010; Smith and Smith 2011). However, in wetland habitats, nonmycorrhizal plants predominate, because mycorrhizal fungi are restricted by low oxygen (Read and Perez-Moreno 2003). Nonmycorrhizal plants have different strategies to take up P, such as root exudation of phosphatase enzymes, which disintegrate organic P (Raven et al. 2018). Such enzymes probably mainly attack labile organic P. For nonmycorrhizal wetland species such as *Carex* spp., excretion of phosphatase enzymes was almost ten times higher for labile forms of organic P than for phytate (Güsewell 2017). Also, *Carex* spp. were able to grow on

labile organic P, but not on phytate (Pérez Corona et al. 1996; Güsewell 2017).

Weak P sorption to Fe-OM complexes in Fe-rich fens

In Fe-rich fens, availability of P to the vegetation probably further increased due to relatively weak P sorption. In fens, P sorption may be relatively weak, because wet conditions lead to reduction of Fe(III) to Fe(II) and lower P-binding capacity (Patrick and Khalid 1974; Emsens et al. 2017). However, as Fe-rich fens also showed high P availability under drained and oxygen-rich conditions (Emsens et al. 2017), this cannot be the only explanation.

In Fe-rich fens, sorption of P is probably also weak due to the high amount of organic Fe + Al, which is part of Fe-OM complexes. Sorption to Fe-OM complexes is weaker than to Fe oxides (Kooijman et al. 2009; Gerke 2010; Gerke 2015). In Fe-OM complexes, organic matter reduces the P-binding capacity, and P is probably mostly bound in monodentate fashion, with only one phosphate oxygen atom bound to an adjacent Fe surface site rather than two (Kim et al. 2011). Possibly, part of the organic Fe + Al consist of fine colloids of iron hydroxide, associated with some OM (Jeanroy and Guillet 1981). However, in soils with high amounts of DOC, such as peat soils, sorption of organic anions to Fe oxides may be rather high, and transform them into Fe-OM complexes (Gu et al. 1994). Also, nonmycorrhizal plants exude large amounts of carboxylates such as citrate and oxalate, as strategy to improve P uptake (Lambers et al. 2008; Raven et al. 2018). These small organic anions can release organic and inorganic P from the P-sorption complex by ligand exchange (Gerke et al. 2000; Johnson and Loepfert 2006; Gerke 2015), but also weaken future P sorption by transforming Fe oxides into Fe-OM complexes (Gu et al. 1994). In any case, organic Fe + Al showed higher correlations with sorbed P and plant P content than inorganic Fe + Al. Also, inorganic Fe + Al only substantially increased in fens with Fe content of 4000 mmol m⁻² in the topsoil or more, while organic Fe + Al already increased at Fe contents of 500 mmol m⁻².

High P in Fe-rich fens does not lead to high biomass

As already mentioned, high availability of weakly sorbed P in Fe-rich fens may especially favour nonmycorrhizal wetland plants. Nonmycorrhizal plants

can mobilize weakly sorbed organic and inorganic P through root exudation of carboxylic anions and ligand exchange (Gerke et al. 2000, Johnson and Loeppert 2006; Gerke 2015), and further increase P-availability through root exudation of phosphatase enzymes, which especially disintegrate labile organic P (Güsewell 2017). Nonmycorrhizal *Carex* spp. may even produce dauciform roots, especially under P-poor conditions, which excrete large amounts of carboxylic anions such as citrate and oxalate (Bakker et al. 2005; Güsewell 2017). High P-uptake capacity by the vegetation was supported by the clear increase in plant P content over the gradient from Fe-poor to Fe-rich fens, and the strong correlation with weakly sorbed (organic) P.

However, while high P-availability in Fe-rich fens clearly resulted in higher plant P uptake, this did not lead to higher aboveground biomass production than in Fe-poor fens. Even in the Netherlands, Fe-rich fens were still mesotrophic and species-rich. Such patterns were also found by Pawlikowski et al. (2013) in pristine fens in Poland, with aboveground biomass around 200 g m^{-2} in both Ca-rich and Fe-rich fens. Emsens et al. (2017) did not report biomass values, but the underlying data revealed that aboveground biomass was 450 g m^{-2} or lower when the two rewetted fens on former agricultural land were excluded, and did not correlate with Fe-content in the soil at all.

Part of the explanation is that Fe-rich fens may be limited by other nutrients than P. In Fe-rich fens, vascular plant N:P ratios ranged around 10 g g^{-1} , which points to N as limiting factor (Olde Venterink et al. 2003). Fe-rich fens may have low N availability due to high microbial respiration and N immobilization even under oxygen-poor conditions, with low net N mineralization as a result (Mettrop et al. 2014). However, in the Netherlands, high atmospheric N deposition probably reduced N limitation to some extent.

Aboveground biomass production in Fe-rich fens may also be reduced by Fe-toxicity. In wetland soils, concentrations of reduced Fe may reach high and toxic levels under oxygen-poor conditions (Patrick and Khalid, 1974; Lucassen et al. 2000), although Fe-rich fens are protected to some extent by the high pH and alkalinity. Also, high Fe tolerance in plant species is associated with low relative growth rates (Snowden and Wheeler 1993).

High P may protect vegetation against Fe-toxicity

High P availability in Fe-rich fens may actually protect the vegetation against Fe-toxicity. High P supply

reduced Fe-toxicity in mesocosm experiments of Wheeler et al. (1985), and may lead to iron phosphate precipitation on the roots, although Fe-tolerant species also reduce Fe toxicity with precipitation of iron oxides by radial oxygen loss (Snowden and Wheeler 1995; Fageria 2001). Also, Fe concentrations in the plant clearly decreased with increasing P concentrations in the nutrient solution (Elliot and Lauchli 1985). High P supply may even lead to Fe deficiency when the latter is in low supply (DeKock and Wallace 1965; Fageria 2001). High P concentrations in the plant may decrease the concentration of active Fe, probably by internal formation of insoluble iron phosphate complexes in the plant cells (Greipsson 1995; Fageria 2001).

Although critical levels for foliar P:Fe ratios have not been established and probably depend on plant species, they indicate to some extent whether plants are affected by Fe deficiency or toxicity. Deficiency of Fe was found for Mustard plants at P:Fe ratios around 140 g g^{-1} (DeKock et al. 1960). In contrast, toxicity of Fe occurred for *Epilobium hirsutum* at P:Fe ratios around 0.1 g g^{-1} (Wheeler et al. 1985). In Lucassen et al. (2000), foliar P:Fe ratios for *Glyceria fluitans* were $0.3\text{--}1.8 \text{ g g}^{-1}$ in sites with Fe toxicity. In our study, P:Fe ratios ranged around 3.3 g g^{-1} in most fens, but between $0.05\text{--}0.1$ in two Fe-rich fens, which may thus be close to Fe toxicity. Nevertheless, the plants looked healthy, and diversity was very high. It is however possible that less Fe-tolerant species, or species with less efficient P uptake do not survive.

Ecological implications

This study shows that Fe-poor fens are P limited, due to low Fe concentrations and low amounts of weakly sorbed (organic) P, independent of Ca richness of the peat soil and potential precipitation of calcium phosphates. This is an advantage, as many characteristic and endangered fen species occur in P limited habitats (Wassen et al. 2005). However, Fe-poor fens are threatened by external P eutrophication, because high P availability to the vegetation is not used to combat Fe toxicity, but for increased plant growth. Nevertheless, low P-sorption capacity in Fe-poor fens may help to reduce P availability once the water quality improves. In the Fe-poor fens of Kooijman et al. (2016), aboveground biomass decreased from 1000 to 250 g m^{-2} within 25 years, and vascular plant N:P ratios increased from 16 to 23 g g^{-1} , which clearly points to lower P availability

(Olde Venterink et al. 2003). Also, eutrophic bryophytes were replaced by more characteristic species such as *Scorpidium scorpioides*.

For Fe-rich fens, high P availability is an inherent characteristic, associated with high amounts of weakly sorbed (organic) P, even in mesotrophic fens with high plant diversity. High P availability in Fe-rich fens does not necessarily lead to high aboveground biomass production, but may instead protect the vegetation against Fe toxicity. However, Fe-rich fens are sensitive to other nutrients, such as N and/or K (Cusell et al. 2014), which may be a problem for fen restoration in former agricultural areas (Emsens et al. 2017). Also, like Fe-poor fens, Fe-rich fens are sensitive to lowered water levels and acidification. However, in undrained situations, Fe-rich fens with high plant diversity and EU-habitat directive species such as *Hamatocaulis vernicosus* may persist even in the Netherlands, as long as buffer capacity and pH remain high enough.

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