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Interferences between root plaque formation and phosphorus availability for isoetids in sediments of oligotrophic lakes

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Abstract. Freshwater isoetids exchanges a high proportion of the photosynthetically produced oxygen over the extensive root system and, therefore, they influence the redox potential (E_h) and phosphorus (P) availability in their sediments. Because isoetids rely on the sediment for P uptake, P may be a key element in controlling the distribution of isoetids. We investigated biomass and P availability to isoetids (*Littorella uniflora* and *Isoetes lacustris*) in a transect of five stations across the littoral zone in oligotrophic Lake Kalgaard, Denmark. At the two shallowest stations (0.6 and 1.0 m depth) the redox potential in the low organic rhizosphere sediment was high (>300 mV) and low concentrations of reduced exchangeable iron (Fe) and manganese (Mn) compounds in the sediment and of precipitated Fe and Mn oxides on isoetid roots (plaques) were found. The concentration of sediment P pools was low and so was isoetid P content and isoetid biomass. At intermediate water depth (1.8 m) sediment E_h was high (∼300 mV) and isoetids showed low root plaque concentrations. However, higher concentration of P pools in the rhizosphere was found at 1.8 m and isoetids showed the highest P content and biomass. At deeper stations (2.8 and 4.6 m depth) E_h was low (<100 mV) in the high organic rhizosphere and high concentrations of plaques were found. The P content in the sediment was high, however, isoetids showed low biomass and low P content. We suggest that the low P content in isoetids growing on P rich organic sediments is partly due to inhibition of the P uptake because of adsorption of P to the oxidized Fe and Mn plaques. However, ratios between oxidized Fe and Fe-bound P, 150 for plaques and 40 for sediment, suggest the isoetids are able to access some of the P that is bound in the plaques. The pools of dissolved P in the porewater were 25–1100 times lower than the estimated annual P requirement for net growth of isoetids while solid fraction P pools were 20–260 times higher than the estimated annual P requirement. Clearly, the oxygen release from isoetid roots decreases the availability of P either by keeping the entire rhizosphere oxidized (low organic sediments) or by the formation of root plaques (high organic sediments).

Key words: iron, *Isoetes lacustris*, *Littorella uniflora*, manganese, phosphorus pools, redox potential

Introduction

Isoetids are a group of small rosette formed macrophytes which are specialized to life in oligotrophic softwater lakes. The plants have a well-developed root system through which nutrients is assimilated from the sediment where the availability is much better than in the water column (Wium-Andersen 1971; Christiansen et al. 1985). Most of the photosynthetically produced oxygen is transported through lacunae to the roots where a major part is released to the sediment (Sand-Jensen et al. 1982; Christensen et al. 1994; Pedersen et al. 1995). The redox potential (E_h) and the biogeochemistry in the rhizosphere sediment is thus influenced by isoetids (Wium-Andersen & Andersen 1972; Christensen & Sørensen 1986; Andersen & Olsen 1994; Christensen et al. 1997).

Plaques, which are coatings of oxidized iron (Fe) and manganese (Mn) compounds on macrophyte roots, can be formed due to root oxygen release (Bacha & Hossner 1977; Chen et al. 1980; Mendelssohn & Postek 1982; St-Cyr & Crowder 1990). In addition, plaques contain a wide range of accessory elements including nutrients and heavy metals (Green & Etherington 1977; Otte et al. 1989; St-Cyr et al. 1993). Most investigations concerning plaques on macrophyte roots have dealt with emergent wetland plants (Mendelssohn et al. 1995). However, visual observations of plaques on submerged isoetid macrophytes have been reported (Wium-Andersen & Andersen 1972; Sand-Jensen et al. 1982; Schuette 1995), and most recently microscopic and energy dispersive spectrometric studies of plaques on roots of the submerged macrophyte, *Vallisneria americana*, (St-Cyr et al. 1993; Wigand & Stevenson 1997) and quantitative analyses of plaques on *V. americana* and *Heteranthera dubia* roots have been published (St-Cyr & Campbell 1996).

A number of biotic and abiotic factors besides root oxygen release controls whether plaques are formed or not. The concentration and the form of Fe in the sediment, and therefore the E_h, are important factors for plaque formations (reviewed by Mendelssohn et al. 1995). At low E_h the reduced soluble form of Fe (Fe(II)) will be present in the sediment and because Fe(II) is soluble, it will diffuse via concentration gradients towards sites of precipitation of the solid oxidized form of Fe (Fe(III)). Sites for Fe(II) oxidation in littoral sediments is normally the upper sediment surface (Boström et al. 1982; Chambers & Odum 1990), however, because of root oxygen release the surface of macrophyte roots can also be sites for Fe(III) accumulation, and thus plaque formations. Besides root oxygen release it has been suggested that enzymatic (Mitsui et al. 1962) and bacterial (Trolldenier 1988; St-Cyr et al. 1993) oxidation can contribute to plaque formations. It has been shown that isoetids grown on sediment with low content of organic matter can oxidize

the whole rhizosphere (Christensen & Andersen 1996). Low concentrations of plaques are expected to be formed under these conditions because Fe in the rhizosphere are present as Fe(III), and Fe(II) diffusion from the deeper sediments will accumulate below the rhizosphere in the horizon between high and low E_h conditions (Tessenow & Baynes 1975, 1978; Christensen et al. 1997). However, in sediments with high content of organic matter the decomposition processes results in productions of reductants and development of anoxia in the root zone and, therefore, a sharp oxygen gradient is developed around the roots and deposition of Fe plaques is expected to occur in this narrow zone (Christensen & Sand-Jensen 1998). Manganese possess the same attributes as Fe but Mn is mobilized easier than Fe, especially under more oxidized conditions (Patrick & Henderson 1981; Christensen et al. 1997) and, therefore, Mn is normally well represented in plaques (Levan & Riha 1986; Christensen & Sand-Jensen 1998) although the concentration of Mn in most sediments is an order of magnitude lower than the concentration of Fe (Bortleson 1974; Young & Harvey 1992).

Since oxidized Fe and Mn compounds are known to have high capacity to bind P (Lijklema 1980; Christensen et al. 1997), the oxygen release from isoetid roots will very likely affect the P availability in their sediments and, therefore, P may be a key element in controlling the distribution of isoetids. Therefore, we measured the biomass and P content of isoetids (*Littorella uniflora* (L.) Ascherson and *Isoetes lacustris* L.) in a transect from shallow to deeper waters across the littoral zone in an oligotrophic lake. We hypothesized the isoetids to decrease the P availability at shallow waters by keeping the entire rhizosphere oxidized (low organic sediments) whereas the P availability to isoetids at deeper waters (high organic sediments) would be more dependant on the presence of root plaques.

Material and methods

Study site

Lake Kalgaard is a small (10.5 ha) shallow (mean depth = 4.65 m) oligotrophic, softwater lake situated in the central Jutland, Denmark (56°1′ N, 9°27′ E). A more detailed description of Lake Kalgaard and its isoetid population is available in Sand-Jensen & Søndergaard (1978, 1979). A transect from shallow (0.6 m) to deeper waters (4.6 m) were investigated in September 1995. The transect was placed in the northeastern part of the lake and four stations vegetated with *L. uniflora* (stations A, B, C, and D), and one station vegetated with *I. lacustris* (station E) were investigated (Figure 1).

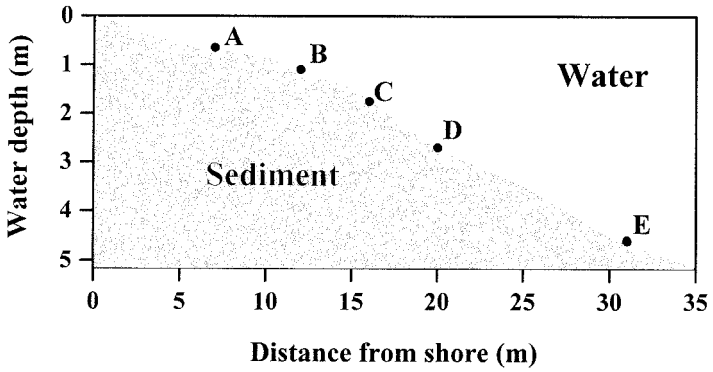

Figure 1. The five stations in the transect investigated in Lake Kalgaard. Stations A, B, C, and D were vegetated with *L. uniflora* whereas the area between station D and E was mainly vegetated with *I. lacustris*. Sediments at water depths deeper than 4.6 m were unvegetated.

Sampling of sediment and porewater

Four sediment cores at each station were collected for E_h profile measurements in the field. Measurements of E_h were performed according to Hargrave (1972) using a platinum electrode with a calomel electrode as a reference. The measurements were performed in daylight and a constant stabilization time of two minutes was used before each reading.

Two profiles of dissolved inorganic phosphorus (DIP) in the porewater was measured at each station using porewater equilibrators (Hesslein 1976; Bottomley & Bayly 1984) with Spectra/Por regenerated cellulose membranes (MWCO 6-8000 Daltons) fastened on both sides of a PVC stake drilled with 2.5 cm holes set at 2.5 cm intervals. The equilibrators were left in the sediment for a week to ensure equilibration after which porewater was sampled in the field.

Three cores (5.2 cm inner diameter) were collected from each of the five stations for analysis of solid pools of Fe, Mn, and P in the sediment. A slightly modified version of a five-step sequential extraction scheme proposed by Psenner et al. (1984) and Jensen and Thamdrup (1993) was used to discriminate between the various pools of Fe, Mn, and P in the sediment. The cores were first sectioned under N_2 atmosphere and pooled for each depth interval (0–2, 2–4, 4–8, 8–12, and 12–16 cm). One gram of fresh wet sediment was first shaken with anoxic 1 M $MgCl_2$ (step 1) to extract exchangeable Fe, Mn and inorganic P (Exc-Fe, Exc-Mn, Exc-IP). Afterwards, the sediment was shaken with bicarbonate-dithionite solution (BD: 0.11 M $Na_2S_2O_4$, 0.11 M $NaHCO_3$, step 2) to extract inorganic P (IP) bound to reducible species of Fe and Mn (Fe-IP) along with the oxidized metal species (Oxid-Fe and Oxid-Mn). The BD-solution seems to be fairly specific for extraction of Fe- and

Mn-bound P in clastic sediments (e.g. Jensen & Thamdrup 1993), and it has also been found to extract about 97% of a freshly formed Fe-oxyhydroxide precipitate. However, some Fe(II) components may be partly leached in the BD-solution (Jensen and Caraco, unpublished). In step 3, Fe, Mn, and IP adsorbed to clay minerals, aluminum oxides and humic-acids were extracted with 0.1 M NaOH. Humic-acid bound Fe, Mn, and P (Hum-Fe, Hum-Mn, Hum-P) were separated from the adsorbed Fe, Mn, and IP (Ads-Fe, Ads-Mn, Ads-IP) by adding 1.5 ml 2 M H_2SO_4 to precipitate humic acids, and subsequently, collecting the precipitate for combustion (520 °C, 2 h) and 1 M hot HCl extraction (Paludan & Jensen 1995). In step 4, the sediment was shaken with 0.5 M HCl to extract acid soluble Fe and Mn and IP bound to calcium (HCl-Fe, HCl-Mn, Ca-IP). Finally in step 5, residual Fe and Mn (Res-Fe and Res-Mn) was extracted with 1 M hot HCl after combustion of the sediment (520 °C, 2 h). The residual P extracted in step 5 was added to the sum of the organic P leached in step 1, 2, and 3. This summed fraction is made up of organic P components (Org-P). Total-Fe (TFe), total-Mn (TMn), and total-P (TP) was determined on parallel sediment samples and pools of P, Fe, and Mn were normalized to these determinations, since they are assumed to be less subject to errors than summing up the different pools measured separately. Dried sediment samples (105 °C, 24 h) were combusted (520 °C, 2 h) to estimate total organic matter content from loss of mass on ignition.

Sampling and analysis of isoetids

At each station three quadrats (510 cm^2) of isoetids were sampled by hand using SCUBA for analysis of isoetid biomass and nutrient content. The isoetids were separated into above ground (leaves and runners) and below ground (roots and stems/corms) samples. The organic dry weight (DW) was measured after drying at 60 °C to constant weight followed by 2 h combustion at 520°C.

Six plants from each station were analyzed for plaques. Whole plants were shaken for one hour in a 20 ml BD solution. The supernatant was collected, and the plants were shaken for an additional hour in 20 ml BD followed by a 5 min shaking in 10 ml distilled water. The final 50 ml solution was aerated for one hour to oxidize the remaining dithionite, and 2 ml 2 M H_2SO_4 was added to keep Fe and Mn in solution. Iron and Mn were then measured on the solution, and the amount of Fe and Mn plaques were expressed per g organic dry weight (DW) of roots. Whole plants were used in the plaque extractions, instead of roots separated from shoots, in order to minimize leaching of P from the plants. There were no indications of plaques on shoots of *L. uniflora*, however, some *I. lacustris* plants showed plaques at the lower part of the leaves and therefore the reported plaque concentrations on *I. lacustris* roots

are probably overestimated. In a control experiment of the plaque extraction method, plaques scraped of *I. lacustris* roots showed that 97.3±0.90% (SE, n = 8) of the TFe in the plaques and 96.6±1.93% (n = 8) of the TMn in the plaques was extracted in the BD shakings.

Chemical analysis

All glassware was washed in 10% HCl before use. Water samples were preserved with 250 μl 2 M H_2SO_4 per 100 ml samples. Dissolved-IP was measured by spectrophotometry as molybdate reactive P. Total-P was measured as DIP after wet oxidation with potassium peroxydisulfate (Koroleff 1983). Organic-P was calculated as the difference between TP and DIP. Total-P content in plant material was extracted with 1 M hot HCl after combustion at 520 °C (Andersen 1976) and measured as DIP. Phosphorus content in plant tissue is expressed as μmol P (g organic DW)$^{-1}$. Total-Fe and TMn in fractionation extracts and in plaque extracts were measured by atomic absorption spectrometry (Perkin-Elmer 2380).

Statistics

For statistical analysis Pearson's correlation test was used. In correlation analyses between isoetid and sediment variables, the mean concentration in the rhizosphere sediment was calculated. The mean root length of *L. uniflora* was 6.5±0.3 cm (mean ± SE, n = 90) and there was no significant difference in root length between the stations. The mean root length of *I. lacustris* was 8.8±0.5 cm (n = 36). Isoetid biomass decreases exponentially with sediment depth and, therefore, the rhizosphere sediment was defined as the sediment depth from 0 to 6 cm which thus represents most of the root biomass (Christensen 1997). Plaque concentrations were compared among the stations with one-way ANOVA followed by multiple unplanned comparison by Tukey's method (Sokal & Rohlf 1995). The data was logarithmic transformed to normalize the distributions and equalize the variance when necessary.

Results

Rhizosphere characteristics

At shallow stations A and B, the sediment was light coloured and sandy at all depths. At station C, the sediment was darker at the surface but light and sandy below 3 cm depth. At deeper stations D and E, the sediment was fine grained and dark at all depths. In the rhizosphere, the DW and the density of

Table 1. Density, dry weight, and organic matter of rhizosphere sediment (0–6 cm) at the four stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). The isoetid roots were not included in the rhizosphere sediment samples. Data represents average values ± SE of 2 or 3 cores.

		Station				
		A	B	C	D	E
Density	(g WW cm^{-3})	2.0 ± 0.22	1.7 ± 0.03	1.6 ± 0.01	1.1 ± 0.00	1.1 ± 0.01
Dry weight	(% of WW)	77 ± 0.6	64 ± 2.3	57 ± 1.0	12 ± 0.5	12 ± 0.7
Organic matter	(% of DW)	0.9 ± 0.22	2.3 ± 0.16	2.5 ± 0.01	20.8 ± 0.86	23.5 ± 1.45

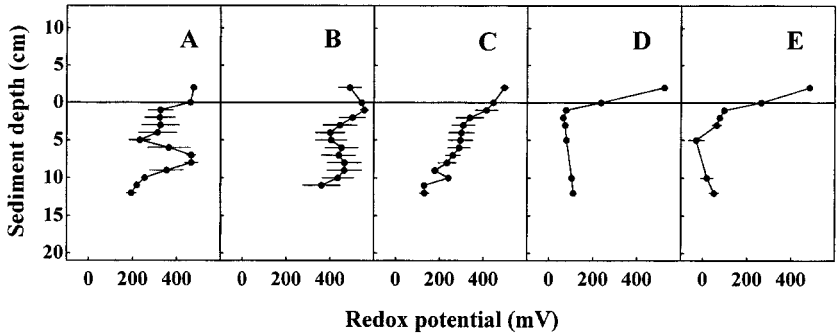

Figure 2. Redox potential of sediment at the four stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). Data represents average values ± SE of four cores.

the wet sediment were highest at the shallow stations (Table 1). The organic content in the rhizosphere was an order of magnitude higher at deeper stations D and E (20–24% of DW) compared to shallow stations A, B, and C (1–3% of DW, Table 1).

Profiles of E_h and DIP

At shallow stations A and B, E_h was high (>300 mV) throughout the sediment cores to a depth of 12 cm (Figure 2). At station C, E_h was high in the upper 5 cm of the sediment, but decreased to values less than 300 mV below this depth. In contrast at deeper stations D and E, E_h was only high in the surface of the sediment and decreased to values below 100 mV at depths deeper than 1 cm.

Porewater concentrations of DIP were generally low at all stations ($\leq$3 μM), but different patterns of distribution with sediment depth and between stations were observed. Very low DIP concentrations (<1 μM) were observed at stations A, B, and C at all depths (Figure 3). At station D, the DIP concen-

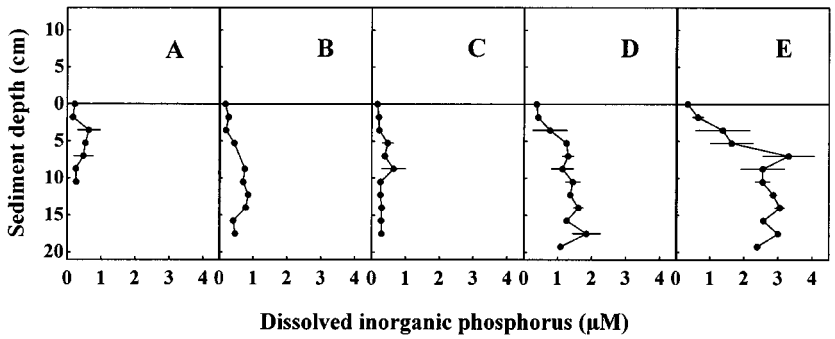

Figure 3. Dissolved inorganic phosphorus of porewater in the sediment measured in samples collected with porewater equilibrators at the four stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). Data represents average values ± SE of two profiles.

tration was higher, especially below 3 cm depth (1–2 μM). At station E, the DIP concentration increased with sediment depth and became constant ($\sim$3 μM) below 10 cm depth. DIP measured in the water column was below the detection limit (0.04 μM).

Solid pools of Fe, Mn, and P in the sediment

The total rhizosphere concentrations of Fe, Mn, and P and the relative distributions of the different pools at each station are shown in Figure 4. The profiles are not shown because of only small changes with sediment depth.

Low concentrations of TFe were observed at stations A and B and higher concentrations at stations C, D, and E. At stations A and B, relative high Oxid-Fe concentrations (30–45% of the TFe concentration) were observed. The rest of the Fe at stations A and B were mainly Res-Fe (40–55%) whereas the concentrations of Hum-Fe ($\sim$6%), HCl-Fe ($\sim$5%), Ads-Fe ($\sim$3%), and Exc-Fe ($\sim$1%) were lower. At stations C and D, Oxid-Fe constituted about 50% of TFe whereas station E showed relatively higher concentrations of Oxid-Fe (45%) in the surface sediment but lower concentrations in sediment depths below 2 cm ($\sim$25%). Also, at stations C, D, and E Res-Fe (20–35%) was present in relative high concentrations. At stations D and E, HCl-Fe (16 and 33%, respectively), Ads-Fe ($\sim$8%), and Hum-Fe ($\sim$6) were found in significant concentrations.

The TMn concentrations were 8–45 times lower than concentrations of TFe. At stations A, B, and C, Oxid-Mn constituted about 90% of TMn and therefore relative low concentrations of the remaining pools were found. Also, at stations D and E Oxid-Mn was the largest Mn-pool (82 and 38%, respectively), however, HCl-Mn (6% and 15%), Res-Mn (4% and 15%) and

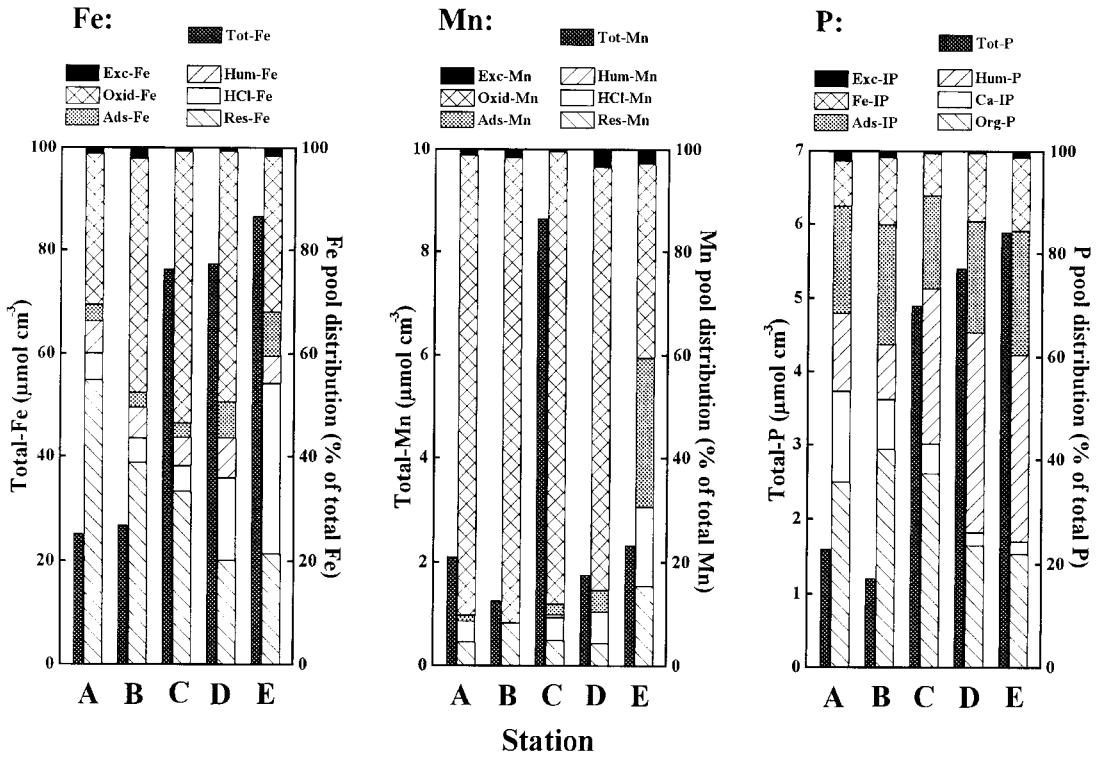

Figure 4. Total-Fe (TFe), total-Mn (TMn), and total-P (TP) and the relative distributions of the Fe-, Mn-, and P pools as an average for the rhizosphere sediment at the four stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). The left axis shows the TFe, TMn, or TP concentration and the right axis shows the relative distributions of the Fe-, Mn- or P pools. Exc-Fe, -Mn, and -IP represents exchangeable Fe, Mn and inorganic phosphorus (IP), Oxid-Fe, -Mn and Fe-IP represents oxidized Fe and Mn compounds and IP bound to oxidized Fe compounds, Ads-Fe, -Mn, and -IP represents adsorbed Fe, Mn, and IP, Hum-Fe, -Mn, and -P represents Fe, Mn, and P bound in humic compounds, HCl-Fe, -Mn, and Ca-IP represents HCl extracted Fe and Mn and calcium bound IP, Res-Fe and -Mn represents residual Fe and Mn and Org-P represents organic P components. All points represent pooled samples from three cores.

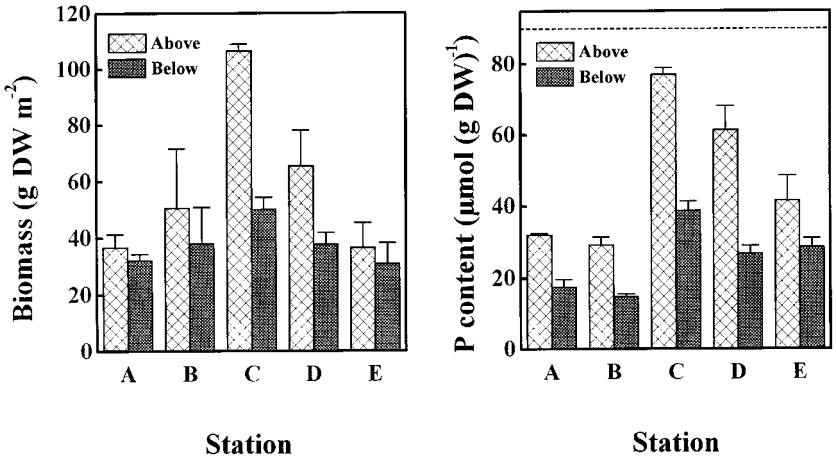

Figure 5. Above and below ground of isoetid biomass (left) and the P content in the above and below ground biomass (right) at the four stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). The data represents average values + SE of three samples. The dashed line represents the critical concentration of 90 μmol (g DW)$^{-1}$ reported for *L. uniflora* (Christiansen et al. 1985).

Ads-Mn (4% and 29%) also made up significant pools. Exc-Mn (∼3% at both stations) and Hum-Mn (<1%) were present in relatively low concentrations.

At stations A and B, the TP concentrations were low (<2 μmol cm^{-3}). Org-P (∼40%) and Ads-P (∼22%) made up the most significant pools at these stations. At stations C, D, and E, the TP concentrations were higher (>4.8 μmol cm^{-3}). Hum-P (∼35%), Org-P (22–37%) and Ads-IP (∼21%) made up the quantitative most important pools at these stations. At all stations low concentrations of Exc-IP, Fe-IP, and Ca-IP were observed compared to Org-P, Ads-P and Hum-P.

Isoetid biomass and nutrient content

The biomass of *L. uniflora* was highest at station C (Figure 5). Also, the *L. uniflora* plants at station C showed higher ratio between above and below ground biomass (2.2±0.14, n = 3) than *L. uniflora* at stations A (1.1±0.08), B (1.3±0.10), and D (1.7±0.21). At station E, the above ground biomass of *I. lacustris* was lower when compared to *L. uniflora* at station D, which resulted in a lower ratio between above and below ground biomass (1.2±0.05) than for *L. uniflora* at station D.

The P content in above ground biomass was higher than in below ground biomass (Figure 5). *Littorella uniflora* at stations A and B showed average tissue P concentrations (∼25 μmol (g DW)$^{-1}$) much lower than the critical concentration of 90 μmol (g DW)$^{-1}$ reported for *L. uniflora* by Christiansen

et al. (1985), however, also at stations C (64±1 μmol (g DW)$^{-1}$)) and D (52±5 μmol (g DW)$^{-1}$)), the P content in *L. uniflora* was lower than the critical concentration. *Isoetes lacustris* at station E, also showed low tissue P concentrations (36±4 μmol (g DW)$^{-1}$)). There was a significant and positive correlation between the P content and the biomass of the above and below ground parts of *L. uniflora* ($p < 0.001$, $r^2 = 0.865$). There was no significant difference in N content in isoetids between stations. On average the N content in the isoetids were 1670±43 μmol (g DW)$^{-1}$ ($n = 15$) which is well above the critical N concentration of 930 μmol (g DW)$^{-1}$ reported for aquatic macrophytes (Gerloff & Krombholz 1966).

Plaques on isoetid roots

The *L. uniflora* roots from stations A, B, and C were white-colored and there were no visible plaque formations on the surfaces of the roots. At station D, thin red-colored plaques (<0.1 mm thick) were visible. Also at station E, plaques on *I. lacustris* roots were general thin although they in some areas reached up to 5 mm thick (these thicker parts of the plaques are called concretions in this paper).

The concentrations of plaques on *L. uniflora* roots increased with the water depth at the stations (Figure 6). Thus, even though plaques were not visible on isoetid roots from stations A, B, and C, the chemical extraction showed that some plaques were present on the roots from these stations, however, the concentrations were generally low (<200 μmol Fe and <70 μmol Mn (g root DW)$^{-1}$). At station D, concentrations of Fe plaques (3500±680 μmol (g root DW)$^{-1}$, mean ± SE, $n = 6$) and Mn plaques (850±270 μmol (g root DW)$^{-1}$) on *L. uniflora* roots were 10 to 100 times higher than observed at the other stations vegetated with *L. uniflora*. Also, *I. lacustris* at station E showed high concentrations of Fe plaques (4100±1820 μmol (g root DW)$^{-1}$) and Mn plaques (680±270 μmol (g root DW)$^{-1}$).

The concentration of Fe and Mn plaques was negatively correlated to E_h (Figure 7; $p = 0.010$, $r^2 = 0.918$; $p = 0.019$, $r^2 = 0.876$, respectively) in the rhizosphere sediment. The concentration of Mn plaques showed significant positive correlation to the concentration of Exc-Mn in the rhizosphere sediment ($p = 0.035$, $r^2 = 0.817$). Also, high Fe plaque concentrations were coincident with high Exc-Fe concentrations in the rhizosphere, however, the correlation was not significant ($p = 0.107$, $r^2 = 0.634$).

Although *I. lacustris* roots were covered with concretions in some areas, the concentrations of Fe and Mn plaques were not significantly higher when compared to the *L. uniflora* roots at station D. This indicates that the plaques on *L. uniflora* roots at station D contained more Fe on a volume basis when compared to the plaques on *I. lacustris* roots. This was also indicated by

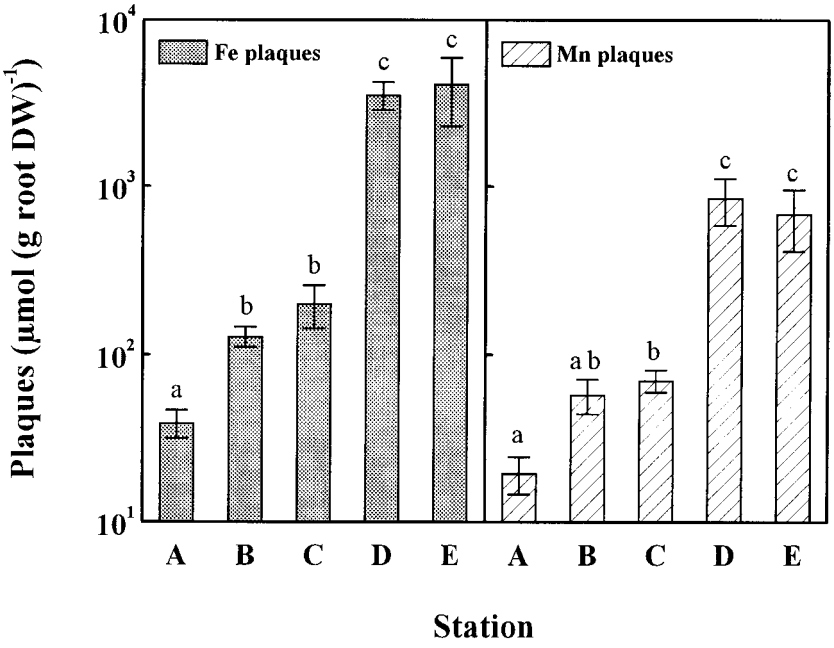

Figure 6. Concentrations of Fe and Mn plaques on isoetid roots at the stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). The data represents average values ± SE of six samples. Values with shared letters are not significantly different ($P > 0.05$).

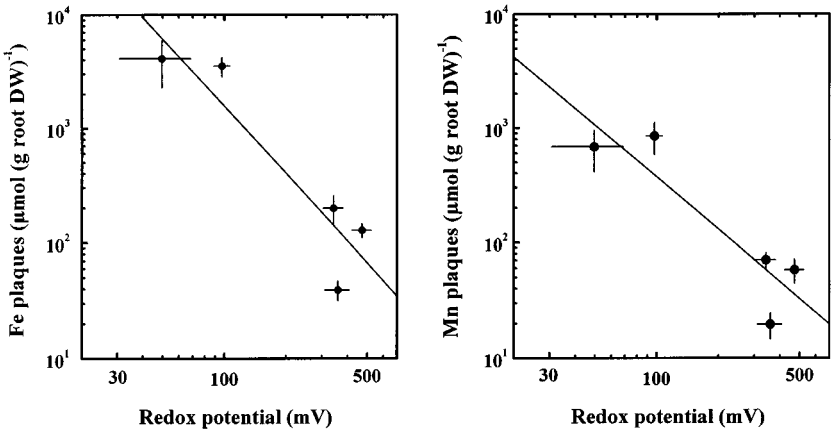

Figure 7. Correlations between the concentration of Fe (left) and Mn (right) plaques on isoetid roots (measured on six samples) with the redox potential (E_h) in the rhizosphere sediment (measured on four sediment cores). The data represents average values ± SE.

analysis of removed concretions from *I. lacustris* roots which showed that only 1.6±0.15% (n = 8) of the concretions weight was composed of Fe(III).

The atomic ratio between Oxid-Fe and Fe-IP (Oxid-Fe:Fe-IP) in the plaques were high for *L. uniflora* at station D (114±19, n = 6) and for *I. lacustris* at station E (174±54, n = 6). The Oxid-Fe:Fe-IP ratio in the removed concretions on the *I. lacustris* roots were much lower (12±2, n = 8) than in the entire plaque. The Oxid-Fe:Fe-IP ratio in the rhizosphere sediment was low (31–52) when compared to the ratios in the plaques.

Discussion

Phosphorus was very likely a limiting factor for biomass development of *L. uniflora* at all stations because the P content in the plants was well below the critical concentration of 90 μmol (g DW)$^{-1}$ reported for *L. uniflora* by Christiansen et al. (1985). Phosphorus limitation was further indicated by the positive correlation between the biomass and the P content of *L. uniflora*. *Isoetes lacustris* at station E showed also low P content, however, to our knowledge no critical concentration have been reported for *I. lacustris* growth and, therefore, it is not possible to evaluate wether this plant species was P limited or not. Light may also be a limiting factor for isoetid biomass development at deeper waters (Sand-Jensen 1978) but still the tissue P concentration decreased at the deeper stations despite the higher concentrations of P in the porewater and in the solid sediment fractions. Similarly, Barko and Smart (1986) found that the biomass of macrophytes decreased with increasing organic matter in the sediment, but also that the production was low on sandy low organic sediments. From fertilization experiments, they concluded that low macrophyte growth on both sandy and organic sediments resulted from nutrient limitation. They explained the observed nutrient limitation with high bulk density and low nutrient availability in nutrient poor sandy sediments whereas the production on organic sediments (low density) was explained by longer mean diffusion distances from solid surfaces to root surfaces and by nutrient complexation to organic matter. Also phytotoxic compounds formed during anaerobic decomposition in organic sediments was suggested to lower the P uptake by macrophytes (see Barko & Smart 1986). In Lake Kalgaard, the isoetid biomass and P content increased with organic matter in the sandy sediments (stations A, B, and C), however, on the high organic, low density sediments (stations D and E) the biomass and P content of the isoetids were low suggesting reduced P availability on these organic but relatively P rich sediments. Some of the mechanisms discussed by Barko and Smart (1986) may be responsible for the low P content in macrophytes growing on organic sediments, however, high root plaque concentrations on macrophytes growing

on reduced organic sediments may also be a likely explanation for the low P availability for the macrophyte.

Factors determining plaque formations

The negative correlations between E_h and the Fe and Mn plaque concentrations suggest that plaques are formed in relatively reduced sediments. This corresponds well with the observed positive relationships between Exc-Fe and Fe plaques and between Exc-Mn and Mn plaques since the Exc-Fe and Exc-Mn fractions represent the exchangeable reduced forms of Fe and Mn in the sediment. Thus, plaques are formed in sediments with relatively low E_h because of high concentrations of reduced Fe and Mn that will diffuse towards the surface of the roots where oxidized Fe and Mn are precipitated because of root oxygen release. The E_h in the sediment will decrease with increasing amounts of organic matter in the sediment but high plant density can increase the E_h because of root oxygen release. The pH in the rhizosphere may also influences the solubility of Fe and Mn (Patrick & Henderson 1981). However, pH was not investigated in this study, because an earlier investigation showed very small changes in pH (about 6) with water depth in the rhizosphere of isoetid vegetated sediments (Wium-Andersen & Andersen 1972).

Our finding that root plaque formations is increased at decreasing redox potentials can probably not be generalized beyond oligotrophic, low sulfate systems, because in systems where sulfate reduction is prevalent, Fe and Mn may be immobilized as sulfide minerals at low redox potentials. Thus, Mendelssohn et al. (1995) hypothesized that Fe plaque formations in wetlands would increase with E_h up to a point where the concentration of Fe in solution would become greatly reduced by Fe-oxyhydroxide formation. Also, Crowder and Macfie (1986) failed to demonstrate a relation between Fe plaques on roots of *Typha latifolia* and E_h.

The influence of plaques on P assimilation

Oxidized compounds of Fe and Mn are known to have high capacity for binding phosphate (Lijklema 1980; Christensen et al. 1997) and, therefore, phosphate assimilation by macrophytes may also be influenced by plaque formations. Howeler (1973) showed that rice plants (*Oryza sativa*) with high root Fe plaque concentrations generally had lower tissue P content than plants with low Fe plaque concentrations. The DIP concentration in the water column of Lake Kalgaard was low. It is therefore reasonable to assume that the major part of the P assimilation by the isoetids occurs over the roots from the sediment/porewater (Carignan 1982; Moeller et al. 1988). *Littorella uniflora* at station D showed lower P content than *L. uniflora* at station C even though

L. uniflora at station D was growing on sediments with higher concentrations of DIP in the porewater. This might suggest that the P assimilation by *L. uniflora* at station D was reduced due to high Fe plaque concentrations. Also, *I. lacustris* with high plaque concentrations at station E showed low tissue P concentrations even though the plants were growing at sediments with relative high DIP porewater concentrations.

The ratio between oxidized Fe and Fe-bound IP (Oxid-Fe:Fe-IP) in *L. uniflora* plaques was high (114) compared to the surrounding rhizosphere sediment (52) at station D, suggesting that *L. uniflora* was able to acquire phosphate bound by oxidized Fe compounds in the root plaques. Also, *I. lacustris* at station E showed high plaque concentrations with a high Oxid-Fe:Fe-IP ratio (174) compared to the surrounding rhizosphere sediment (31) and the more distinct concretions (11). Wigand and Stevenson (1997) also showed a higher Fe:P ratio in Fe plaques of *V. americana* roots compared to the rhizosphere sediment. They suggested that the Fe plaque may act as a phosphate trap available for phosphate assimilation by the macrophytes. In addition, they found a high mycorrhizal infection of the *V. americana* roots and suggested that the phosphate trapped in the plaques may be acquired by fungal symbionts and transported to the plant. Mycorrhizal infection in the studied transect was high for *L. uniflora* at all stations whereas *I. lacustris* showed somewhat lower infection (Wigand et al. 1998). In addition, bacterial association with plaques of submerged macrophytes have been observed (St-Cyr et al. 1993) which may facilitate plant uptake of P bound to oxidized Fe compounds (Craven & Hayasaka 1982; Jansson 1987). However, our results suggest that the overall effect of plaques on macrophytes roots is an inhibition of the P uptake which is in agreement with results from a laboratory study by Christensen and Sand-Jensen (1998) who showed reduced P assimilation as a consequence of plaque formations on the roots of the isoetid macrophyte *Lobelia dortmanna*.

P pools in the rhizosphere sediment and annual P requirement by isoetids

The annual P requirements of the isoetids can be calculated from the P content in isoetids combined with literature values on biomass turnover. Sand-Jensen and Søndergaard (1978) have reported the annual turnover of *L. uniflora* to be 150% (for both roots and leaves) and an annual turnover of *I. lacustris* roots and leaves of 98% and 65%, respectively. Sand-Jensen and Søndergaard (1978) found no difference in leaf turnover rates of *L. uniflora* on sand or moderately organic sediments and, therefore, the same turnover rate of 150% for *L. uniflora* are used at all stations vegetated with *L. uniflora*. The annual turnover rates for porewater DIP can thus be estimated from the DIP content in the rhizosphere (0–6 cm) porewater per unit area. This calculation showed

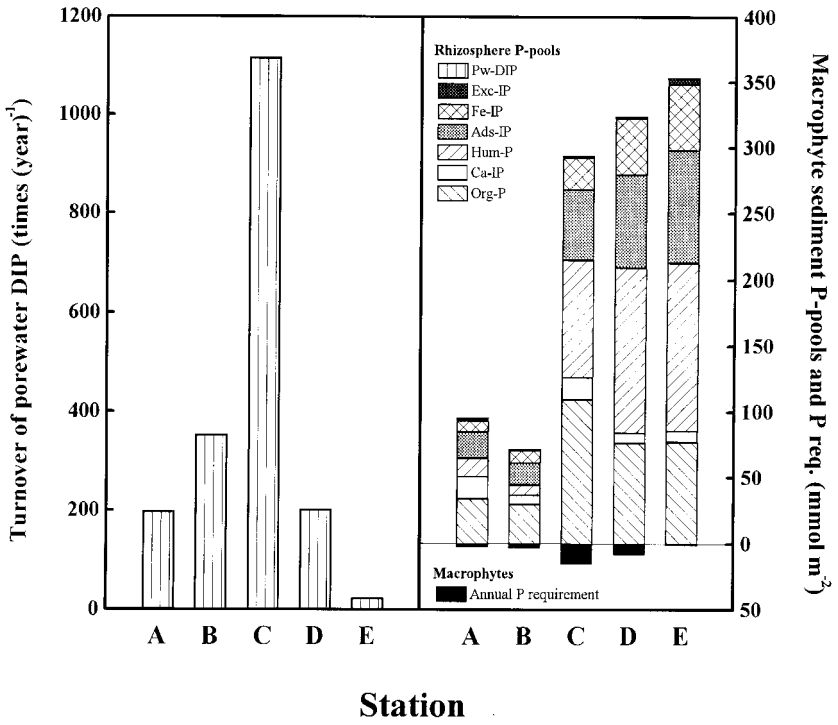

Figure 8. Annual turnover times of dissolved inorganic phosphorus (DIP) (left) and yearly isoetid P requirement compared with the concentrations of P pools available in the rhizosphere sediment (right) at the stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E). Pw-DIP represents porewater phosphate. For description of the other P pools see Figure 5.

high turnover rates of the porewater DIP at the stations vegetated with *L. uniflora* (Figure 8). Thus, station C showed a 1100-fold turnover of the porewater DIP per year whereas stations A, B, and C showed lower turnover rates (200–350 times year^{-1}), but still high compared to the DIP turnover at station E vegetated with *I. lacustris* (25 times year^{-1}). Thus, it is obvious that P has to be supplied from one or more of the solid P pools in the rhizosphere sediment to the isoetids during a growth season.

When comparing the annual P requirements of the isoetids with the concentrations of the P pools in the rhizosphere (0–6 cm) sediment per unit area, the annual P requirements of the isoetids appear low (1–15 mmol m^{-2}) compared to the concentrations of Fe-IP, Ads-IP, Hum-P, and Org-P in the sediment (Figure 8), meanwhile, not all the P pools may be available for macrophyte nutrition. Few investigations exist where the availability of sediment P pools to macrophytes are studied (Boström et al. 1982). How-

ever, Ads-IP, Ca-IP, and Res-P are considered as relatively immobile P pools whereas porewater DIP, Exc-IP, Fe-IP, and Org-P are considered relatively available P pools (Li et al. 1974; Prentki 1979; Pettersson et al. 1988; Psenner & Pucsko 1988). Thus, even though the sediment in Lake Kalgaard has a fairly low P concentration the sediment contains sufficient P to supply many years of isoetid growth.

Plaques on isoetid roots and the significance of plaques for sediment Fe and Mn biogeochemistry

Plaque concentrations are normally expressed as amount of Fe per g root DW and therefore a direct comparison of the plaque concentrations on root surfaces is not possible between different species because macrophytes have differently surfaces to volume ratios. However, the concentration of Fe plaques on *L. uniflora* roots, expressed on root biomass basis, at station D and *I. lacustris* at station E were high compared to values reported for wetland macrophytes. Iron plaques on wetland plants seem not to exceed 1500 μmol (g root DW)$^{-1}$ (Chen et al. 1980; McLoughlin et al. 1985; Macfie & Crowder 1987; St-Cyr & Crowder 1989) whereas *L. uniflora* and *I. lacustris* at stations D and E showed values at about 3500 μmol (g root DW)$^{-1}$. Similar to the present study, St-Cyr and Campbell (1996) found Fe plaque concentrations on roots of the submerged macrophyte *V. americana* at about 3500 μmol (g root DW)$^{-1}$. Thus, submerged macrophytes seem to be able to accumulate more Fe per g root biomass than emergent wetland plants which are probably because submerged plants have thinner roots. Mn plaques on *L. uniflora* and *I. lacustris* at stations D and E also showed higher values than reported for wetland plants (St-Cyr & Crowder 1990; Crowder & Coltman 1993).

From the root biomass and the Fe and Mn plaque concentrations the total amount of Fe and Mn plaques per m^2 sediment can be calculated and compared with the total amount of oxidized Fe and Mn compounds per m^2 rhizosphere (0–6 cm) sediment at the stations (Table 2). This calculation shows that the amount of Fe and Mn plaques of *L. uniflora* roots per m^2 were low ($<$1% and $<$4%, respectively) compared to the amount of oxidized Fe and Mn present in the rhizosphere sediment at stations A, B, and C. However, for *L. uniflora* at station D and for *I. lacustris* at station E, concentrations of Fe and Mn plaques were significant compared to the amount of Oxid-Fe and Oxid-Mn in the rhizosphere sediment (7.5 and 4.7%, respectively, for Fe plaques and 33.5 and 19.5% for Mn plaques). St-Cyr and Campbell (1996) calculated the amount of Fe plaques on *V. americana* roots to be 4.5 and 10.4 mmol Fe m^{-2} at two stations in a river system which is about 10 times lower than the concentrations for *L. uniflora* at station D and *I. lacustris* at station E. The higher concentration of plaques on isoetid roots is probably caused

Table 2. The concentrations of iron (Fe) and manganese (Mn) plaque on isoetid roots per m^2 sediment compared to the concentrations of oxidized Fe and Mn compounds (Oxid-Fe and Oxid-Mn) in the rhizosphere sediment (0–6 cm) per m^2 at the four stations vegetated with *L. uniflora* (A, B, C, and D) and at the station vegetated with *I. lacustris* (E).

		Station				
		A	B	C	D	E
Plaque Fe	(mmol m^{-2})	1	3	7	102	43
Rhiz. Oxid-Fe	(mmol m^{-2})	245	404	1396	1254	874
Plaque Mn	(mmol m^{-2})	0.4	1.3	2.5	24.4	7.3
Rhiz. Oxid-Mn	(mmol m^{-2})	63.2	38.4	256.1	48.6	29.7

by the relatively high root biomass of isoetids. Thus, isoetids growing in fairly reduced sediments are capable of influencing the sediment Fe and Mn biogeochemistry due to plaque formation, whereas isoetids growing in low organic sediments will oxidize the whole rhizosphere and therefore change the Fe and Mn biogeochemistry both in and below the rhizosphere sediment (see also Tessenow & Baynes 1975, 1978; Christensen et al. 1997). Wetland macrophytes have also been reported to change the biogeochemistry of Fe in rhizosphere sediments due to Fe plaque formations, thus Chen et al. (1980) estimated that *O. sativa* roots at maturity would contain about 540 mmol Fe plaque m^{-2}.

Concluding remarks

The extensive release of oxygen from isoetid roots seemingly decreases P availability for nutrition in both low and high organic sediments by inducing a precipitation of oxidized Fe∼P complexes. In sandy, low organic sediments, P is probably taken up directly from the porewater and the P availability is therefore set by the rate of dissolution of solid P fractions. This dissolution rate may be enhanced by release of organic acids either directly from the roots or from associated mychorrhizal fungi as it has been reported for terrestial plants (Lambers & Poorter 1992) and as an indication of this mechanism, high concentrations of dissolved organic carbon were observed in the porewater from the sandy stations (see Holmer et al. 1998; Wigand et al. 1998). In reduced organic rich sediments, extensive root plaque formations interrupts P diffusion from the porewater to the roots. Although this inhibits macrophyte P uptake, Fe-bound P in plaques may still be available for macrophytes as it is indicated by the much higher Fe:P ratio in the root plaques than in the

surrounding sediment. The influence of root plaques on macrophyte P uptake was notable even if the root plaques made up less than 10% of the oxidized iron present in the rhizosphere sediment.

The indications provided in this study of how root plaque formations may alter nutrient availability for macrophytes calls for more studies of plaque abundance and effects in littoral zones of lakes, in general. At present, quantitative analyses of plaques on roots of submerged aquatic macrophytes has only been reported for*V. americana* (St-Cyr & Campbell 1996), *H. dubia* (St-Cyr & Campbell 1996), *L. uniflora* (this study), and *I. lacustris* (this study).

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