

Implications of soil organic carbon and the biogeochemistry of iron and aluminum on soil phosphorus distribution in flooded forests of the lower Orinoco River, Venezuela

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Abstract. Relationships among soil phosphorus distribution, soil organic carbon and biogeochemistry of iron and aluminum were studied along a flooded forest gradient of the Mapire river, Venezuela. Soil samples were collected during the dry season in three zones subjected to different flooding intensity: MAX inundated 8 months per year, MED inundated 5 months per year, and MIN inundated 2 months per year. Total labile phosphorus (resin + bicarbonate extractable fractions) was significantly higher in MIN than in MAX. The longer non-flooding period in MIN probably allowed a higher accumulation of microbial biomass in soils of this zone and consequently a greater release of the bicarbonate organic fraction. The moderately labile phosphorus fraction associated with the chemisorbed phosphorus on amorphous and some crystalline aluminum and iron was significantly lower in MAX than in MIN following the same tendency observed for crystalline iron oxides. This result allowed us to hypothesize that the combined effect of a long flood period and a high soil organic carbon content in the MAX, could be appropriate conditions for microbial reduction of stable forms of iron. The ratio of soil organic carbon to total organic phosphorus decreased from MAX to MIN, indicating higher mineralization of organic phosphorus in MIN. Our results suggest two distinct flood-dependent mechanisms operating for phosphorus release along the gradient. In MAX mineralization process appears to be limited, while microbial mineral dissolution appears to be an important source of phosphorus. In MIN supply of phosphorus is associated with the stability of soil organic matter.

Introduction

Extensive areas of river watersheds in the tropics are covered with forests, some of which are seasonally flooded following the pattern imposed by the river hydrology (Kubitzky 1989). These forests are characterized by annual oscillations between aquatic and terrestrial phases, and the pulsing of the river discharge is the major driving force responsible for the structure, function and evolutionary history of the biota in these ecosystems (Junk et al. 1989).

During the aquatic phase, water restricts the gas diffusion in the soil and can limit the soil oxygen availability (Smith and Tiedje 1979). Depletion of soil

oxygen diminishes the redox potential (Gambrell and Patrick 1978) with consequent impacts on the composition and activity of the soil microbial communities (Magnunsson 1992, 1994), mineral dissolution (Lovely et al. 1991, 1993; Baldwin and Mitchell 2000), and nutrient availability (Silver et al. 1999; Miller et al. 2001; Shuur and Matson 2001).

In flooded soils the phosphorus (P) cycle is closely related to the cycling of iron (Fe) and aluminum (Al) (Patrick and Khalid 1974; Darke and Walbridge 2000). Transformations of Fe are largely controlled by the soil redox potential (Darke and Walbridge 2000). Low redox potential promotes the microbial reduction of Fe(III) oxides (Lovley et al. 1991; Baldwin et al. 1997; Baldwin and Mitchell 2000). Under such circumstances the phosphate anion chemically sorbed to these iron oxides surfaces is released when the surface is reduced (Baldwin and Mitchell 2000).

During the terrestrial phase the oxygen availability increases and the principal effect will be the oxidation of previously reduced iron minerals to amorphous ferric oxyhydroxides (Baldwin and Mitchell 2000). These ferric oxyhydroxides have a large surface area and consequently a high affinity for P (De Groot and Fabre 1993; Baldwin 1996).

The seasonally changes in the water availability can also alter the P cycle by affecting the stability of the organic matter. Anaerobic conditions associated with flooding can restrict the organic matter decomposition (Gale and Gilmour 1988; Updegraff et al. 1995), while soil desiccation during the dry phase produces the death of the microbes (Qiu and McComb 1995).

Because the P cycle is not yet well understood in tropical seasonally flooded forests, and taking into account that the seasonality can be playing an important role not only in the stability of the soil organic matter and the biogeochemistry of Fe and Al but also in the soil P partitioning, we addressed this study to determine the relationships among soil P distribution, soil organic carbon and Fe and Al chemistry along a tropical seasonally flooded forest gradient.

Methods

Study area

The floodplain of the Mapire River is located in SE Venezuela, between 7°30'–8°30' N and 64°30'–65°00' W. This river is a northern tributary of the lower Orinoco River, and its basin constitutes a region of low relief covered by the Pleistocene Mesa Formation, which consists of horizontally bedded alluvial sediments and to a minor extent by marsh deposits (Carbón and Schubert 1994).

The Mapire river has been classified as black-water river due to its brown color and its oligotrophic character in terms of nutrient, sediment load and primary productivity (Vegas-Vilarrúbia 1988). According to the climatic

diagram of the region (Vegas-Vilarrúbia and Herrera 1993), the annual mean temperature is 27.4 °C and the annual precipitation averages 1333 mm, with the dry season between November and April and the rainy season from May to October.

Forests communities at the Mapire river are related to longitudinal and perpendicular gradients of flooding depth and duration, which are associated with local topography. The soil samples were collected in three zones along a flooded gradient perpendicular to the course of the Mapire River: (i) a low zone near the river margin (MAX), where the flood reaches a maximum of up to 12 m and lasts up to 8 months (from May to December); (ii) an intermediate zone (MED) where the flood reaches a maximum of up to 5 m and lasts up to 5 months (from June to November); and (iii) a high zone (MIN) where the flood reaches a maximum of 1 m for 2 months (from July to September).

Soil sample collection

The soil samples were regularly collected from the surface mineral horizon (0–10 cm) at eight points arranged into four transects in the MAX and MED zones and at six points from three transects in the MIN zone. The samples were taken with an auger during the dry season (March 2003). Each soil sample was air dried before chemical analysis.

P fractions determination

P fractions were obtained using the method of Hedley et al. (1982) as modified by Tiessen and Moir (1993). This method uses a sequence of increasingly strong reagents to successively remove more recalcitrant fractions of inorganic (Pi) and organic (Po) phosphorus. Such fractions are associated with operationally defined pools: (i) P extracted with resin that is often considered the labile Pi; (ii) the bicarbonate- and hydroxide-extractable P considered as the Fe- and Al-associated Pi; and (iii) the hot concentrate HCl and digestion of the residue defined as the highly resistant and unavailable Pi. The difference between the total P and Pi of each extract gives the Po (Tiessen and Moir 1993).

Duplicate 0.50 g aliquots of the soil sample were extracted sequentially by anion exchange resin, followed by 0.5 M NaHCO₃, 0.1 M NaOH, hot concentrated HCl and final complete digestion of the residue in concentrated H₂SO₄ and H₂O₂. Total P was determined in aliquots of each extract by digestion with ammonium persulphate and H₂SO₄ to convert all the organic P (Po) forms to inorganic P (Pi) forms. Another subsample of each extract was used to measure Pi after acidification with H₂SO₄ to precipitate the organic matter. The pH of the final extracted solutions was adjusted and the P concentration was determined colorimetrically by the molybdate–ascorbic acid procedure of Murphy and Riley (1962).

Al and Fe fractions estimation and soil organic carbon determination

A selective dissolution method was used to estimate concentrations of non-crystalline, crystalline and organically bound forms of Al and Fe in these soils. Organically bound Fe and Al were determined by extracting the soil with sodium pyrophosphate (Fe_P , Al_P) (McKeague 1967). Poorly crystalline forms of Fe and Al (Fe_O , Al_O) were obtained after extraction with ammonium oxalate (McKeague and Day 1966). Highly structured Fe and Al associated to crystalline Fe oxides were extracted with dithionite–citrate–bicarbonate (Fe_{DCB} and Al_{DCB}) following the method of Mehra and Jackson (1960). It is known that the oxalate extract dissolves both non-crystalline and organically bound Fe and Al forms, while the DCB method dissolves crystalline Fe and Al associated, non-crystalline and organically bound Fe and Al forms. Therefore estimates of the different forms of Fe and Al were obtained using the following relationship: non-crystalline Fe and Al forms (Fe_O , Al_O) = oxalate – pyrophosphate extract crystalline Fe and Al associated (Fe_{DCB} , Al_{DCB}) = DCB – oxalate extract

Fe and Al concentrations were determined using atomic absorption spectroscopy. Soil organic carbon was determined using the Walkley and Black (1934) titration method. All chemical analysis were performed in duplicate and judged satisfactory if the results were within 5% error.

Statistics analysis

Statistical analysis of the data was carried out by an one-way analysis of variance (ANOVA). A Tukey Honest Significant Difference (HSD) test was used when statistical differences ($p < 0.05$) were observed. Simple linear correlations were used to assess the relationship among soil P fractions, soil organic carbon (SOC) and Fe and Al fractions, and tested for significance at the 5% level. All statistics were computed using STATISTICA for Windows 6.0 (Statistica 2001).

Results and discussion*Relationships between soil P fractions and the biogeochemistry of Fe and Al*

The values of resin extractable Pi throughout the flooded gradient (Table 1) were lower than the values reported for other black water river floodplain soils ($10\text{--}11\text{ mg kg}^{-1}$) (Stanturf and Schoenholtz 1998). No significant differences ($p > 0.05$) were found in resin extractable and bicarbonate-Pi fractions among the different zones of the gradient (Table 1). However, the concentration of total labile forms (resin + $NaHCO_3$ -Pi + $NaHCO_3$ -Po), considered as the total P immediately available to the plants (Cross and Schlesinger 1995), was

Table 1. Soil phosphorus fractions (mg kg^{-1}) in the studied zone along the flooded forest gradient.

	MAX	MED	MIN
Resin-Pi	4.46 \pm 2.22a	3.24 \pm 1.60a	2.68 \pm 1.10a
NaHCO ₃ -Pi	6.23 \pm 3.00a	10.95 \pm 5.74a	11.77 \pm 3.24a
NaOH-Pi	31.44 \pm 12.42b	70.05 \pm 19.50a	81.02 \pm 21.89a
HCl _(conc) -Pi	15.29 \pm 2.01b	18.84 \pm 2.21a	21.05 \pm 4.83a
Residual-P	162.25 \pm 15.21a	171.95 \pm 20.66a	128.33 \pm 3.75b
NaHCO ₃ -Po	9.56 \pm 3.89b	11.30 \pm 5.00ab	17.75 \pm 7.68a
NaOH-Po	12.58 \pm 9.19a	16.64 \pm 14.22a	20.80 \pm 16.48a
HCl-Po	6.91 \pm 4.76a	5.41 \pm 2.78a	6.67 \pm 5.04a
Total-P (Σ)	248.71 \pm 21.68b	308.38 \pm 38.34a	290.07 \pm 37.66ab
Total labile-P	20.25 \pm 4.86b	25.49 \pm 3.78ab	32.20 \pm 8.81a

MAX – maximum zone; MED – medium zone; MIN – minimum zone; Pi – inorganic phosphorus; Po – organic phosphorus. Total labile-P = resin-Pi + NaHCO₃-Pi + NaHCO₃-Po. Mean values \pm SD followed by the same letter in each line are not different at $p > 0.05$ according to the Tukey's test.

significantly lower ($p < 0.004$) in the MAX zone than in the MIN zone (Table 1). The NaHCO₃-Po fraction plays an important role in the total labile P of the studied soils (Table 1), representing 47, 44 and 55% of the total labile P fraction in the MAX, MED and MIN zones, respectively. This NaHCO₃-Po fraction was significantly higher ($p < 0.032$) in the MIN zone than in the MAX zone, and was responsible for the higher value of total labile P in the MIN zone (Table 1).

The larger accumulation of soil Po that was observed in the NaHCO₃-Po fraction of the MIN zone compared to the MAX and MED zones might be explained as the consequence of a larger accumulation of microbial biomass that can occur during prolonged dryness and its subsequent release by the end of the dry period. Turner and Haygarth (2001) have suggested that the increase in the total amount of water soluble P that is usually observed after drying soils can be attributed to the direct release of P from microbial biomass. In fact, other studies have indicated that the large P flush observed during the re-wetting of soils is associated with the lysis of microbial cells induced by soil dryness (Qiu and McComb 1995). It is very likely, that the extended non-flooded period to which our soils from the MIN zone were subjected before the sampling, allowed the built up of enough microbial biomass to account for the increase of Po in the NaHCO₃-Po fraction of the soil from this zone.

Even though there is little doubt on the effect that the microbiota exerts in the spatial variability of the total labile P concentration, other factors associated with the soil mineralogy throughout the gradient can be affecting the dynamics of P in this total labile fraction. Non-crystalline oxides of Fe and Al are considered the main sorbents of phosphate in flooded soils (Kuo and Mikkelsen 1979; Richardson 1985; Sah and Mikkelsen 1986), due to their comparatively large specific surface area in relation to the crystalline forms (Parfitt 1989; Baldwin 1996). Along the flooded gradient no significant changes

Table 2. Soil chemical properties in the studied zones along the flooded forest gradient.

	MAX	MED	MIN
%SOC	2.38 ± 0.52a	2.14 ± 0.38a	1.32 ± 0.21b
Fe _O	7.99 ± 4.09a	5.80 ± 2.53a	10.59 ± 7.31a
Fe _{DCB}	20.70 ± 5.02b	26.22 ± 4.85b	57.39 ± 15.43a
Al _O	b.d.l.	b.d.l.	b.d.l.
Al _{DCB}	b.d.l.	8.61 ± 20.40b	57.71 ± 16.19a
Fe _P	21.29 ± 6.01b	29.48 ± 5.42a	31.84 ± 4.68a
Al _P	99.65 ± 35.36b	141.76 ± 33.85a	174.01 ± 19.01a
Fe _O /Fe _{DCB}	0.43 ± 0.30a	0.23 ± 0.11a	0.23 ± 0.21a

MAX – maximum zone; MED – medium zone; MIN – minimum zone; Fe_O-Al_O, Fe_{DCB}-Al_{DCB} and Fe_P-Al_P – ammonium-oxalate, dithionite-citrate-bicarbonate and pyrophosphates-extractable Fe or Al, respectively (mmol kg⁻¹); SOC – soil organic carbon (%); b.d.l. – below the detection limit. Mean values ± SD followed by the same letter in each line are not different at $p < 0.05$ according to the Tukey's test.

in the content of amorphous Fe oxides (Fe_O) were obtained, and amorphous Al oxides (Al_O) were not detected (Table 2). However when the three zones were combined a positive and significant correlation between crystalline Fe oxides (Fe_{DCB}) and total labile-P ($r^2 = 0.6489$; $p < 0.0005$) was obtained. This results allow us to suggests that crystalline Fe oxides could be controlling the retention of the bio-available P in these soils.

In flooded soils several mechanisms have been connected with the P release from the geochemical pools, namely reduction or dissolution of Fe(III) phosphates, hydrolysis and dissolution of Fe and Al phosphates and release of clay-associated phosphates through anionic exchange (Ponnamperuma 1972). However, some authors have indicated that the microbial reduction of Fe(III) oxides is one of the main mechanisms associated to this release (Lovley et al. 1991; Baldwin et al. 1997; Baldwin and Mitchell 2000).

In order to understand the potential effect that the differential length of flooding periods can have on the distribution of P along soils of the studied zones (MIN, MED and MAX), we focused our attention on those P fractions that are sensible to the redox processes, such as the labile NaOH-Pi. The moderately labile NaOH-Pi fraction has been associated with the strongly P chemisorbed on amorphous and some crystalline Al and Fe phosphates (Tiessen et al. 1983), consequently, any change occurring in the behavior of Fe and Al oxides during anoxic periods should be reflected on the size of this P fraction. Because our results showed a significant increase of P in the NaOH-Pi fraction going from the MAX to the MIN zones (Table 1) we hypothesized that the low content of this labile fraction observed in the MAX zone, should be associated with the P that is released from the geochemical pool during the microbial reduction of Fe(III) oxides.

It has been indicated that the poorly crystalline hydrous ferric oxide is the principal form of Fe(III) oxide reduced by bacteria (Lovley and Phillips 1987;

Zachara et al. 1998), because these surfaces require less activation energy (Munch and Ottow 1984). In this study the content of amorphous Fe oxides does not change along the flooded gradient, suggesting that the poorly crystalline oxide surfaces are not being affected by the length of the flooded period.

Changes in the crystalline Fe(III) oxides (Fe_{DCB}) followed similar trends as the NaOH-Pi fraction (Tables 1 and 2). The content of the crystalline Fe(III) oxides in the MAX and MED was significantly lower than in the MIN zone ($p < 0.05$). There is considerable doubts about the type of Fe(III) that can be used by microbes in sedimentary environments and it had been shown that crystalline Fe(III) forms are not important electron acceptors for the Fe(III) respiring microorganisms (Lovley 2000). However, our results seems to suggest that in our system Fe(III)-respiring microorganisms might be using the crystalline Fe(III) oxides as an electron acceptor. The combined effect of a longer flooded period and a higher soil organic carbon content in the MAX zone, could be allowing the microbial reduction of stable forms of Fe. In order to demonstrate this hypothesis further laboratory studies are required.

Another important P fraction that could be sensitive to changes in the soil oxygen availability in the soil is the highly resistant HCl-Pi fraction. This P fraction was significantly lower ($p < 0.05$) in the MAX zone than in the MED and MIN zones (Table 1). This result contributes to support our hypothesis and suggests that probably the higher intensity of mineral dissolution processes in the MAX zone has caused the liberation of P from the more recalcitrant pool. However, the shorter dry season in the MAX zone is probably not enough for the process of occlusion of P, while the longer dry season in the MIN zone could cause the mineral aging and decrease the potential for P release from the geochemical pool. It is known that the desiccation of soil promotes the process of mineral aging (Lijklema 1980; Mitchell and Baldwin 1998)

In the studied soils poorly crystalline aluminum oxides (Al_O) were not detected and the Al associated to Fe oxides (Al_{DCB}) was only obtained in the MED and MIN zones, with a high spatial variability in MED (Table 2). The inconsistent tendency observed for both P and Al elements, did not allow us to associate the soil P variations with the biogeochemistry of Al oxides. In flooded environments the Al chemistry is not affected by the changes redox potentials and its dynamics is controlled by the tendency of Al to form complexes with the soil organic matter (Darke and Walbridge 2000). It is probably that in the studied soils the formation of humus-Al complexes has prevented the precipitation of the poorly crystalline Al oxides, such as has been discussed by Velbel (1985).

Our results of the Al associated to the Fe oxides (Al_{DCB}) are not clear. However we thought that in the MAX zone the Fe(III) dissolution process generated released of Al which was exported farther away from the river margin as organic complex.

Humic-(Fe, Al) complexes are active surfaces that control the P sorption capacity in acid soils. Gerke and Hermann (1992) have discussed that the humic-Fe complexes show a considerably higher P-adsorption capacity than

the amorphous Fe oxides. Along the studied soil gradient organically bound Fe fraction (Fe_p) significantly increased from the MAX to the MIN zone (Table 2). In the MAX zone the content of the NaOH-Pi was significantly and positively correlate with the content of Fe_p ($r^2 = 0.5977$; $p < 0.0245$), while in the MIN zone no significant correlation between both parameters was obtained ($r^2 = 0.1297$; $p > 0.4831$). The significant and positive relation obtained in MAX suggests that the P released from the geochemical pool can partly be retained within the system as a humic-Fe- PO_4 complex. The organically bounded Al fraction (Al_p) showed the same tendency as observed for the Fe_p (Table 2). However we did not find significant statistical evidences that support the role of the organically bound Al surfaces in the retention of P throughout the gradient.

Relationships between soil P fractions and soil organic matter stability

The differentiated conditions of intensity and duration of the anaerobiosis process throughout the flood gradient appear to control the P supply by affecting the mineral stability and the soil organic matter turnover. We hypothesized that in the MAX zone where the flood reaches up to 12 m and last up to 8 months per year, P is supplied from the mineral-bound pools, while in the MIN zone, where the water level increases just 1 m and lasts only 2 months per year, the source of available P is organic.

As it was previously discussed, the liberation of P from the microbial biomass is an important source of available P in the MIN zone. The ratio of the organic carbon to the total organic P (C/ P_o) was used in this study to estimate the mineralization potential of organic phosphorus. This ratio decreased from 876.27 in the MAX zone to 383.01 in the MIN zone (Table 3). P organic mineralization occurs at C/ P_o ratios below 200 while immobilization processes occur when the ratio up to > 300 (Dalal 1977). According to our results (Table 3), mineralization of organic P appears to be more favored in the MIN zone than in the MED and MAX zones.

Under anaerobic conditions the mineralization of nutrients from decomposing soil organic matter is restricted, causing an increase in the soil organic carbon (Gale and Gilmour 1988; Updegraff et al. 1995; Shuur et al. 2001). However, the variation of the soil organic carbon (SOC) is also controlled by

Table 3. Soil organic carbon/total organic P (SOC/ P_o) ratio in the studied zones along the seasonal flooded forest gradient.

	MAX	MED	MIN
Maximum values	1523.13	2209.30	772.43
Minimum values	518.95	314.17	171.40
Mean \pm SD	876.27 \pm 349.36	847.18 \pm 597.88	383.01 \pm 242.20

MAX – maximum zone; MED – medium zone; MIN – minimum zone.

the soil mineralogy (Torn et al. 1997; Miller et al. 2001). When the data of the three studied zones were combined, a negative correlation between SOC and the total iron content ($\text{Fe}_\text{O} + \text{Fe}_\text{DCB}$) was obtained ($r^2 = 0.4641$; $p < 0.0005$). This result is in agreement with those obtained by Miller et al. (2001), and suggests that important amounts of C can be released during the microbial reduction of Fe(III) oxides, which can contribute with the high content of the SOC in the MAX zone.

From the discussed results, it is clear that two distinct flood-dependent mechanisms for P release are operating along the gradient. Therefore an obligate question arises: Are the plants along the flood gradient taking up P in differentiated form? We did not evaluate the content of P in the biomass. However Rosales (1990) reported high P concentrations in the leaves of several species growing in the MAX and MED zones, as well as an increase in the sclerophilic character from the MAX to the MIN zone. Finally it is important to emphasize that our results are restricted to single sampling date and ignored the effect of the water seasonality on the stability of mineral soils and turnover of soil organic carbon.

Conclusion

The movement and distribution of the soil phosphorus in the seasonally flooded gradient of the Mapire river are linked to the flooding intensity. In the longer term flood zone the mineralization process appears to be limited, while the microbial mineral dissolution of Fe oxides appears to be an important source of this nutrient. The humus-Fe complexes play an important role in the P retention within this zone. In the shorter flood zone with a subsequent larger dry period, the soil organic matter turnover appear to control the soil P supply. Changes in the flood patterns could bring serious implications in the flow of P and C of these forests and consequently in the primary productivity.

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