



Effects of flooding on phosphorus and iron mobilization in highly weathered soils under different land-use types: Short-term effects and mechanisms



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ABSTRACT

The strong affinity of phosphorus (P) to iron (Fe) oxides and hydroxides in highly weathered tropical soils limits P availability and therefore plant productivity in tropics. In flooded soils, however, P fixed by Fe oxides and hydroxides can be released into more available forms because of Fe^{3+} reduction to Fe^{2+} . These P dynamics in flooded soils are well documented for rice paddies. Such effects are much less studied in other land-use types influenced by seasonal flooding, especially in the tropics during heavy monsoon rains. The aim of this study was to investigate the P mobilization during flooding leading to anaerobic conditions in topsoil and subsoil depending on land-use type. Samples were collected in highly weathered Acrisols from four replicate sites under natural rainforest, jungle rubber, rubber and oil palm plantations in Sumatra, Indonesia. Topsoil and subsoil were taken to ensure a wide range of soil organic matter (SOM) and P contents. Soils were incubated under anaerobic, flooded conditions at $30 \pm 1^\circ\text{C}$ for 60 days. Our results confirmed the hypothesis that soil flooding mobilizes P and increases P availability. Two distinct and opposite periods were observed during the flooding. During the first three weeks of flooding, the dissolved P (DP) concentration peaked, simultaneously with the peak of dissolved Fe^{2+} (DFe^{2+}) and dissolved organic carbon (DOC). After three weeks, P availability in soils decreased, although Fe-P (P_{NaOH}) and available P ($\text{P}_{\text{NaHCO}_3}$) did not reach the initial, pre-flooding levels. The impacts of flooding on P and Fe forms was strong in the topsoil, where P dissolution and availability were generally higher under forest and, to a lesser extent, under jungle rubber. A positive correlation between DOC and DFe^{2+} ($R^2 = 0.42$) in topsoil indicates that the intensity of microbially-mediated Fe^{3+} reduction is limited by the amount of available carbon (C) as an energy source for microorganisms and as electron donor. Microbial mineralization of organic P from SOM also increases P availability, and this process requires available C. This interpretation was supported by the strong correlation ($R^2 = 0.58$) between available P and DOC, as well as between DP and DOC ($R^2 = 0.56$) in topsoil. The increasing pH in topsoil and subsoil after flooding of all land-use types may also influence the P release over time. In summary, the increase of available P and DP during flooding is due to three main mechanisms: (1) P release via the microbially-mediated reductive dissolution of Fe^{3+} oxides; (2) P release during SOM mineralization and (3) solubility of Fe phosphate due to increasing pH. These mechanisms are relevant not only in riparian areas, where flooding occurs, but also in soils waterlogged after regular heavy rainfalls during the wet season. Therefore, we speculate that the P turnover is faster in compacted soils under plantations because of regular changes of oxic and anoxic conditions. Consequently, more P is pumped by the vegetation and then removed from plantations due to yield export.

1. Introduction

Phosphorus (P) in most soils and especially in the tropics is limited

for plant uptake due to its immobilization on iron (Fe) and aluminum (Al) oxides (Dieter et al., 2010; Holford, 1997; Maranguit et al., 2017). These bonds are very stable. Nonetheless, P sorption with Fe oxides

Abbreviations: P, phosphorus; Fe-P, Fe-bound phosphorus; DOC, dissolved organic carbon; DFe^{2+} , dissolved Fe^{2+} ; DP, dissolved phosphorus; SOM, soil organic matter; C, carbon

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might be reversible under anaerobic conditions, e.g., after flooding (Parker and Beck, 2003; Ponnampereuma, 1972; Rakotoson et al., 2015, 2016). Large seasonal fluctuations in rainfall, typical of tropical forested ecosystems, can change available P and are highest directly after the onset of the wet season (Wood et al., 2015; Wood and Lawrence, 2008). Flooding increases the available P content by 1.4–60 mg P kg⁻¹ compared with aerobic soils (Rakotoson et al., 2014). This is indicated by the increase of extractable P such as NaHCO₃-extractable P (Verma and Tripathi, 1982; Zhang et al., 2003).

Once flooded, soils rapidly become anaerobic, resulting in a decline in the redox potential (Eh) (Ponnampereuma, 1972). The microbial community structure shifts to microbes capable of anaerobic respiration (Unger et al., 2009). Microorganisms utilize alternative electron acceptors such as NO₃⁻, Mn⁴⁺, Fe³⁺ and SO₄²⁻ to maintain their metabolism (Loeb et al., 2008; Unger et al., 2009). They use the electron acceptor that yields the highest energy or that is most readily available. In highly weathered acidic soils, Fe³⁺ hydroxides are very abundant. Thus, microorganisms such as *Geobacter sulfurreducens* (Sánchez-Alcalá et al., 2011) will use Fe³⁺ as the terminal electron acceptor (Weber et al., 2006). Hence, Fe³⁺ will be reduced to Fe²⁺, releasing substantial quantities of associated P (Amarawansa et al., 2015; Loeb et al., 2008; Ponnampereuma, 1972). Therefore, the P concentration in the soil solution will increase together with soluble Fe²⁺ (Kirk, 2004; Quintero et al., 2007). This mechanism, leading to an increase of P and Fe solubility under anaerobic respiration, is known as microbially-mediated reductive dissolution of Fe³⁺ oxides.

The amount of P released into the soil solution depends on: soil characteristics involved in reduction processes: 1) abundance of Fe oxides and their crystallinity; 2) soil organic matter (SOM) content and its microbial availability as electron donors (Quintero et al., 2007; Scalenghe et al., 2002); 3) total P content and its forms (Amarawansa et al., 2015) and 4) soil pH neutralization as a result of soil flooding, which increases the P availability by increasing the solubility of Fe- and Al-P compounds in acid soils (Chacon et al., 2005; Zhang et al., 2003). Additionally, SOM is used as a source of carbon (C) and energy by microorganisms to fuel and stimulate the microbially-mediated reductive dissolution of Fe³⁺ minerals (Rakotoson et al., 2015; Scalenghe et al., 2002; Zhang et al., 1994). Hence, we hypothesize that P released by Fe³⁺ reduction is stimulated in soil with high labile C availability. Furthermore, we hypothesize that P release is influenced by land-use changes because of their impacts on SOM and P contents.

Land-use conversion is the predominant global change in this century, driven by the high demand for food, fiber and other products (Geissen et al., 2009; Guillaume et al., 2015). In the tropics, for example in Indonesia, agricultural intensification is ongoing mainly for rubber and oil palm at the expense of primary and secondary forest (Gibbs et al., 2010; Guillaume et al., 2016). Forest conversion in general, strongly changes soil physical, chemical and biological properties (Geissen et al., 2009; Moges et al., 2013) as well as ecosystem functioning (Barnes et al., 2014) especially after conversion to rubber and oil palm monoculture plantation. Indeed, almost 70% SOC in the topsoil of oil palm and rubber plantations has been lost compared to rainforest in Indonesia (Guillaume et al., 2015). P forms changes from easily available to non-available forms due to P fixation by Fe and Al oxides. Organic P which is considered as reserve pool buffering available inorganic P becomes depleted and total P decreases after conversion of forest to oil palm and rubber plantations (Maranguit et al., 2017). Moreover, rubber and especially oil palm plantations suffer from soil compaction, resulting in higher bulk density and less water infiltration (Guillaume et al., 2016; Merten et al., 2016). Plantation soils are therefore quickly waterlogged by regular heavy rainfalls. This results in a series of biogeochemical changes that profoundly influence P status and availability. No studies are available on transformed systems in Sumatra, Indonesia, in particular studies focusing on the mobilization of P forms (Fe-bound P) that are normally retained by well-drained soils when these become partly waterlogged or flooded by regular heavy

rainfalls during the wet season. Moreover, most of the literature on Fe dynamics and P availability after soil flooding pertains to rice paddies (e.g., Ponnampereuma, 1972; Rakotoson et al., 2015; Zhang et al., 2003).

In this study, we investigated the effects of flooding on the P and Fe dynamics in topsoil (0–10 cm) and subsoil (20–30 cm) horizons of Acrisol under forest, agro-forest (jungle rubber) and monoculture plantations of rubber and oil palm on Sumatra, Indonesia. The study was designed to assess changes in Fe and P solubility and mobility under flooded anaerobic incubation. We hypothesized that under flooding: (1) Fe³⁺ will be reduced to Fe²⁺, thereby liberating P adsorbed on Fe³⁺, as indicated by P in the solution and NaHCO₃-Extractable P in the soil; (2) the content of P bound to Fe oxides, which is measured by NaOH-Extractable P, will decrease; and (3) Fe²⁺ and P in the soil solution will increase and will be higher in the topsoil under forest and jungle rubber, which have a higher SOM content than soils under monoculture plantations.

2. Materials and methods

2.1. Study site and soil sampling

The soil samples were collected in the lowland of Jambi Province in Sumatra, Indonesia. The climate is tropical humid with an average temperature of 27 °C and an average precipitation of 2200 mm year⁻¹ and 112–259 mm month⁻¹ (Guillaume et al., 2015). Experiments were carried out in (1) tropical rainforest and three land-use types dominating in the study region: (2) jungle rubber, (3) rubber plantations and (4) oil palm plantations. Jungle rubber is an extensively-managed agroforest in which rubber trees are planted in a partially logged forest. Rubber and oil palm plantations were intensively managed monocultures. Rubber and oil plantations were mature plantations of 15 and 14 years old in average, respectively, while jungle rubber were older than 20 years old. The region is covered by tertiary sediments (Barber et al., 2005). Sites ranged between 50 and 100 m a.s.l. Soils were well-drained Acrisols according to the World reference Base classification with sandy loam texture. Further description of the study site is available in Guillaume et al. (2015).

To assess the effects of soil flooding on P mobilization, four replicate sites for each land-use type were selected. At each site, samples were collected in the topsoil (Ah horizon; 0–10 cm) and in the subsoil (20–30 cm) by digging a pit. These topsoil and subsoil samples were taken to ensure a wide range of soil properties with regard to SOM and P content (Table 1). Soil samples were air-dried and sieved at 2 mm. Plant debris and stones, if present, were removed.

2.2. Soil flooding and incubation

2.5 g of soil sample were filled into a 12 ml glass tube (Labco Exetainer). Six milliliters of purified distilled water were added in each tube and air was driven out by purging N₂ gas. The suspension was then covered with a rubber stopper to prevent O₂ diffusion, evaporation losses and to ensure anaerobic conditions. Four field replicates of each land-use type and depth for each determination were incubated in the dark at 30 ± 1 °C. Directly after water addition (1 h) and after 7, 14, 21, 28, 45, and 60 days of continuous soil flooding, samples were shaken and pH was determined. Then, samples were filtered using a syringe filter with 0.45 µm pore size (Labsolute, Germany). The extracts for dissolved P (DP) and dissolved Fe²⁺ (DFe²⁺) determination were acidified immediately with 1 ml of 0.1 M HCl per 2 ml of solution to prevent oxidation. The remaining extracts were analyzed for dissolved organic C (DOC) (see Section 2.3). The samples were further analyzed for available-P and Fe-P (see Section 2.4).

Table 1
Characteristics of the soils use (means \pm SE; n = 4).

Land-use	Soil parameter				
	pH 1:2.5	C (%)	Avail-Pi ^a (mg kg ⁻¹)	Fe-Pi ^b (mg kg ⁻¹)	HCl-Fe(II) (mg kg ⁻¹)
Topsoil (0–10 cm)					
Forest	3.8	6.77 \pm 0.64	10.0 \pm 0.10	15.9 \pm 0.41	2.01 \pm 0.25
Jungle rubber	4.2	4.03 \pm 0.57	5.03 \pm 0.85	17.6 \pm 0.49	5.23 \pm 0.19
Rubber	4.4	2.56 \pm 0.32	7.13 \pm 0.65	18.2 \pm 0.72	5.02 \pm 0.26
Oil palm	4.3	2.05 \pm 0.47	8.49 \pm 1.16	16.9 \pm 0.51	3.68 \pm 0.20
Subsoil (20–30 cm)					
Forest	4.5	0.55 \pm 0.18	5.73 \pm 0.76	5.49 \pm 0.38	2.02 \pm 0.51
Jungle rubber	4.4	0.74 \pm 0.30	4.37 \pm 0.15	8.22 \pm 0.91	3.23 \pm 0.19
Rubber	4.3	0.87 \pm 0.19	3.61 \pm 0.29	9.23 \pm 0.53	2.02 \pm 0.65
Oil palm	4.3	0.62 \pm 0.18	3.35 \pm 0.36	8.59 \pm 0.62	1.68 \pm 0.70

^a Available inorganic P that was extracted using 0.5 M NaHCO₃ at pH 8.5.

^b Fe-bound inorganic P that was extracted using 0.1 M NaOH.

2.3. Determination of DOC, DP and DFe²⁺ in the soil solution

Dissolved C was measured using a ‘multi N/C 2100’ (Analytik jena) analyzer. Dissolved C corresponds to DOC because no carbonates were present in the soil (Guillaume et al., 2015).

DP was determined by the malachite green (MG) colorimetric method (D’Angelo et al., 2001; Yevdokimov et al., 2016). Briefly, 150 μ l of extracts was mixed with 30 μ l of the first reagent (ammonium molybdate tetrahydrate and sulfuric acid) in disposable sterile 96-well polystyrene microtiter plates (Puregrade, Germany). These plates were shaken for 10 min on an orbital shaker at low speed (< 90 rev min⁻¹).

Thereafter, 30 μ l of the second reagent, which was a mixture of MG carbinol hydrochloride and polyvinyl alcohol (Sigma Aldrich Co), was added. The plate was shaken for an additional 20 min. After shaking, samples were exposed to 40 °C for 40 min. To decrease variability between the replicates, microplates were left overnight at room temperature. Thereafter, absorbance was read using a spectrophotometer (TECAN; Infinite M200 pro) with 630 nm wavelength. Standards were also prepared in triplicate and treated the same way as the samples.

Fe²⁺ was determined by ferrozine assay (Stookey, 1970). In principle, the Fe²⁺ ions in the solution form complexes with the ferrozine and form a magenta-colored solution. In brief, 1 ml of extract was

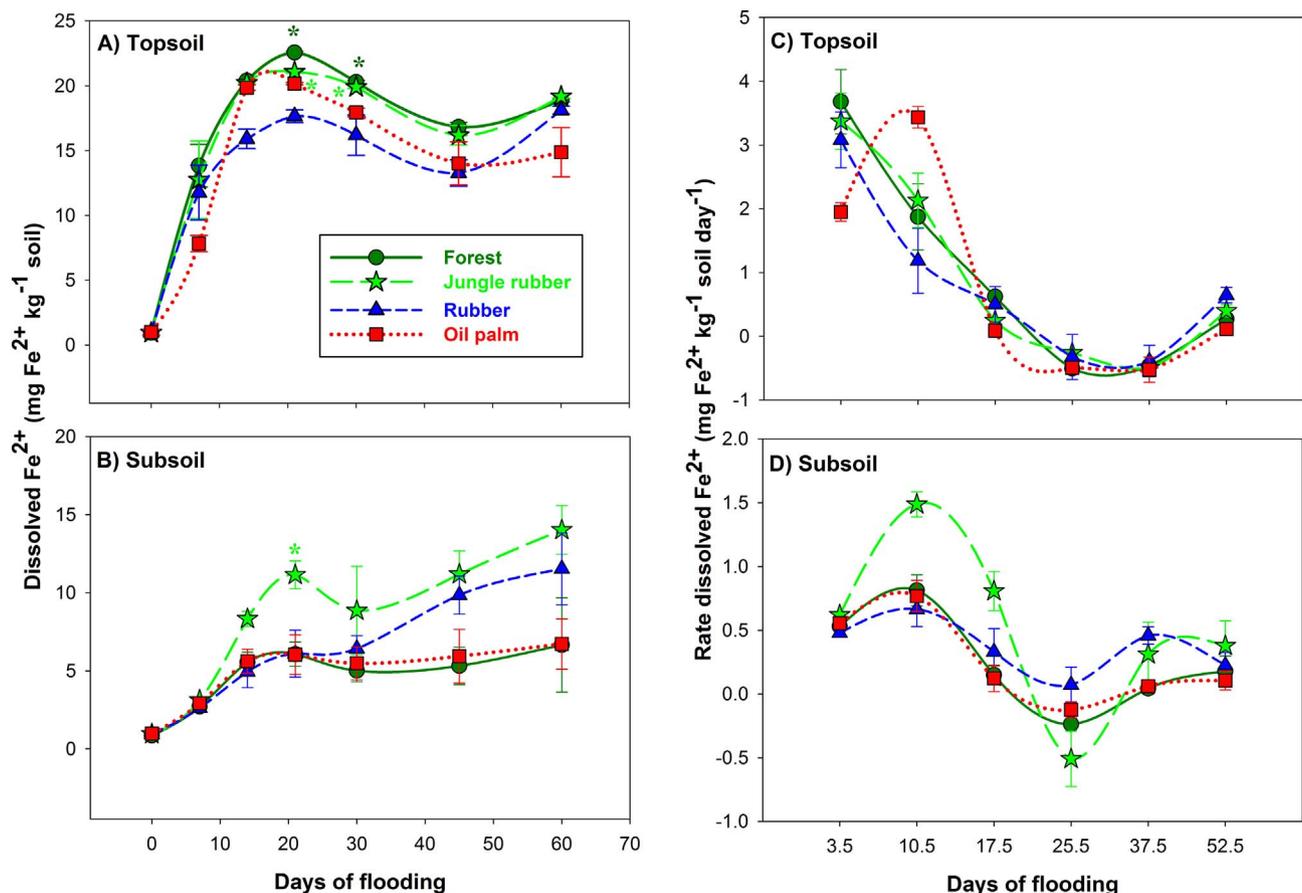


Fig. 1. Effects of soil flooding on DFe²⁺ under forest, jungle rubber, rubber and oil palm plantations. We compared the DFe²⁺ of the topsoil (A) and subsoil (B). The computed rates of DFe²⁺ production in the topsoil (C) and subsoil (D) are also shown. DFe²⁺ on day 0 indicates the initial content determined after 1 h of soil flooding. Values represent means \pm SE (n = 4). Asterisks in (A) and (B) show significant differences (one-way ANOVA; p < 0.05) to rubber and oil palm soils at a given sampling time.

mixed with 100 μl ferrozine solution and then with 50 μl buffer solution (ammonium acetate adjusted to pH 9.5 with ammonium hydroxide) in a 24-well polystyrene microplate (Puregrade, Germany). Then, the microplate was read in a spectrophotometer (TECAN; Infinite M200 pro) with 562 nm wavelength after color developed fully, normally after 5 min.

2.4. Determination of available-P and Fe-P in the soil

Soil samples after filtration were measured for NaHCO_3 - and NaOH -extractable P. In this experiment, NaHCO_3 -extractable P and NaOH -extractable P refer to available-P and Fe-bound P (Fe-P), respectively. The available-P and Fe-P was assessed following the Hedley P fractionation method (Hedley et al., 1982; Maranguit et al., 2017). Briefly, 1 g of wet soil sample was placed into a 50 ml screw cap centrifuge plastic tube. Samples were sequentially extracted with 30 ml of 0.5 M NaHCO_3 (pH 8.5) to extract available-P and, thereafter, with 0.1 M NaOH to extract P bound with Fe. Samples were shaken for 16 h in an orbital shaker, centrifuged at 3500 rpm for 10 min and then filtered. Phosphorus was determined in all extracts and standards by the malachite green colorimetric method (D'Angelo et al., 2001; Yevdokimov et al., 2016) (as mentioned in Section 2.3).

2.5. Data analysis

Results of all parameters were expressed as the mean of four field replicate samples and were presented as mg kg^{-1} or mg g^{-1} of the dry fine earth (< 2 mm) fraction. Normality and homogeneity of variance were checked using Shapiro-Wilk's W test and Levene tests, respectively. Differences of the soil parameter between land-use types for each sampling period were tested using one-way analysis of variance (ANOVA). To check the influence of land-use on the changes of soil parameters between two time points, two-way repeated measures ANOVA were tested with (4) land-use and (2) time as the factors. For the changes between two sampling periods of one land-use, single sample t -tests (testing means against zero) on the rate of DFe^{2+} , DP and DOC were conducted. A t -test result not significantly different to 0 means no changes between the two sampling period. Relationships between P availability indices (i.e., avail-P, Fe-P, DP) and associated soil parameters (i.e., DOC, DFe^{2+}) were evaluated using Multiple Linear Regression. Relationships between two parameters were tested on the values recorded after 21 days of soil flooding; the time when Fe^{2+} reduction and P release peaked. Significance was accepted at a probability level of $p \leq 0.05$. All statistical analyses were carried out using STATISTICA 12 (StatSoft Inc., USA)

3. Results

3.1. Fe^{3+} reduction and Fe^{2+} mobilization

The Fe^{2+} concentration in the soil solution was used as an index of Fe^{3+} reduction (Stookey, 1970). An increasing concentration of DFe^{2+} in the soil solution (Fig. 1) indicates the intensity of reduction. Soil flooding reduces Fe^{3+} to Fe^{2+} under anaerobic conditions already within a few days. The reduction of Fe^{3+} to Fe^{2+} had already started one week after soil flooding, as highlighted by an increased ($p < 0.001$) DFe^{2+} concentration after 7 days (Fig. 1).

DFe^{2+} in topsoil reached its maximum after 21 days of flooding in all land-use types. The highest DFe^{2+} peak ($p < 0.05$) was in forest ($22.6 \pm 0.1 \text{ mg Fe}^{2+} \text{ kg}^{-1}$), followed by jungle rubber ($21.1 \pm 0.1 \text{ mg Fe}^{2+} \text{ kg}^{-1}$), oil palm ($20.2 \pm 0.1 \text{ mg Fe}^{2+} \text{ kg}^{-1}$) and rubber ($17.6 \pm 0.5 \text{ mg Fe}^{2+} \text{ kg}^{-1}$) (Fig. 1). The highest Fe^{2+} production rate was about 4 days after soil flooding in all land-use types except for oil palm, in which highest production occurred at about 11 days. Note, however, that the DFe^{2+} production in all land-use types diminished over time until the last flooding day. In fact, the rate was

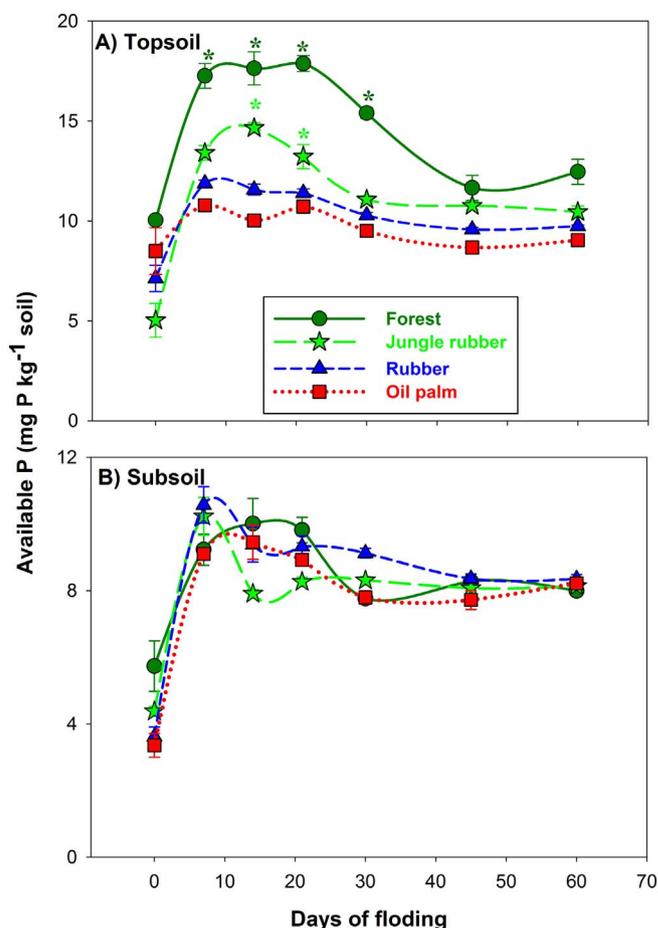


Fig. 2. Effects of soil flooding on the available P ($\text{P}_{\text{NaHCO}_3}$) of topsoil (A) and subsoil (B) under forest, jungle rubber, rubber and oil palm plantations. Available P on day 0 indicates the initial content before soil flooding. Values represent means \pm SE ($n = 4$). Asterisks show significant differences (one-way ANOVA; $p < 0.05$) to rubber and oil palm soils at a given sampling time.

negative between days 26 and 38 of flooding (t -test; $n = 4$; $p < 0.05$), indicating re-precipitation of DFe^{2+} .

In contrast, subsoils reached their maximum accumulation of DFe^{2+} in the last week (60 days) of soil flooding in all land-use types, showing that reduction processes in the subsoil were slower. The highest production rate of DFe^{2+} in subsoil was recorded about 11 days after flooding (Fig. 1). Jungle rubber showed higher rates ($p < 0.05$) than other land-use types throughout the soil flooding period.

In all land-use types, topsoil had higher ($p < 0.01$) DFe^{2+} than subsoil throughout the flooding period (Fig. 1). This shows that the DFe^{2+} production rate is much faster in the topsoil, indicating the importance of SOM and microorganisms in Fe reduction.

3.2. Phosphorus mobilization and availability

Soil flooding increases P availability ($p < 0.05$), as shown by the increase of NaHCO_3 -extractable P in both topsoil and subsoil in all land-use types after one week of flooding (Fig. 2). The available P content of the forest and jungle rubber topsoil started to increase after the first week of soil flooding and continued until it peaked after 21 days, i.e. at the same time when the DFe^{2+} (Fig. 1) in the soil solution was at its maximum. The maximum increase of available P in forest (21 days = $17.9 \text{ mg P kg}^{-1} \pm 1.6$) and jungle rubber (14 days = $14.7 \text{ mg P kg}^{-1} \pm 1.0$) was about 50–70% of the initial content before flooding (Fig. 2). Forest and jungle rubber had higher ($p < 0.05$) available P compared to monoculture plantations throughout the flooding period. In contrast, the topsoil of monoculture

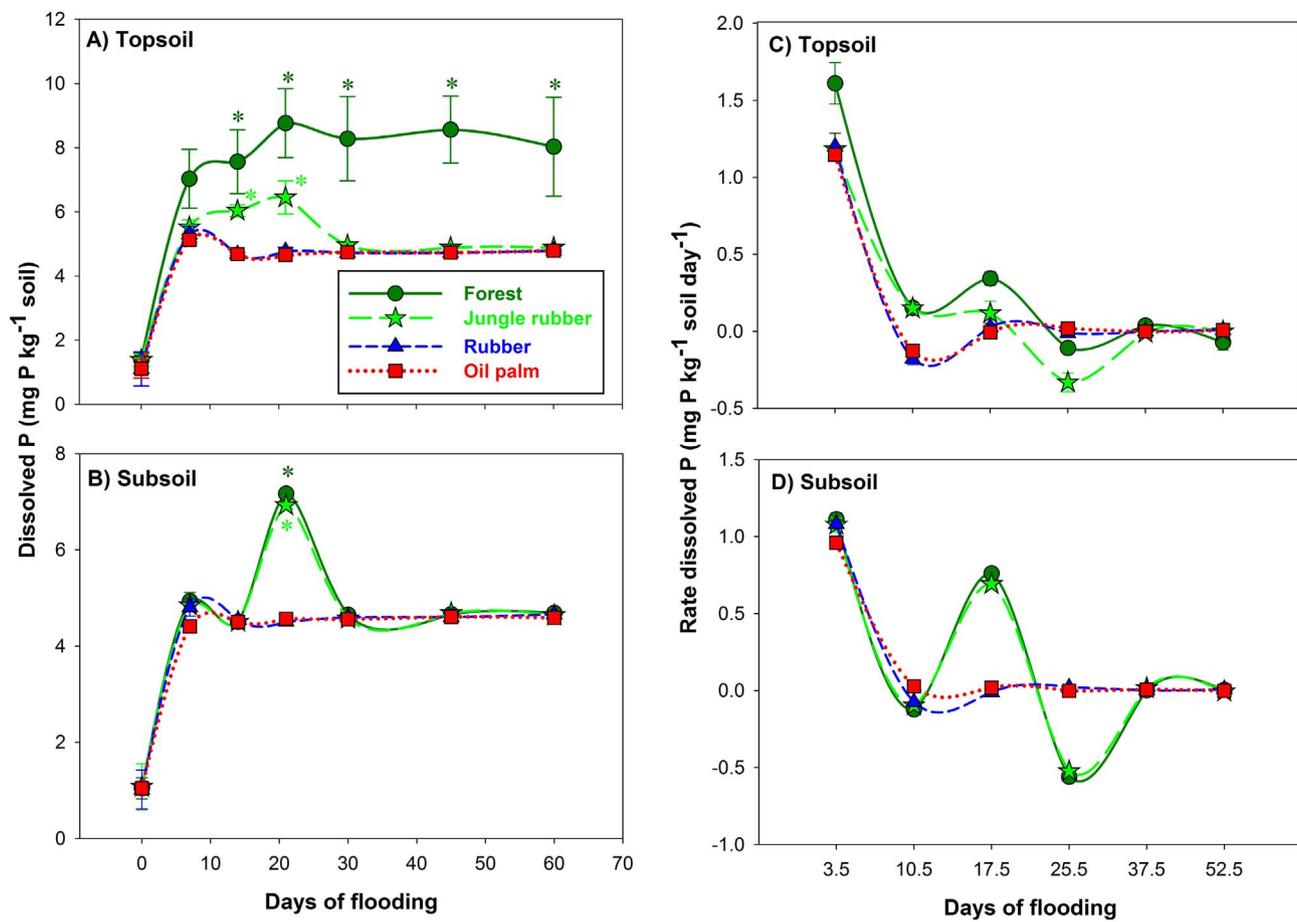


Fig. 3. Effects of soil flooding on DP under forest, jungle rubber, rubber and oil palm plantations. We compared the DP of the topsoil (A) and subsoil (B). The computed rates of DP production in the topsoil (C) and subsoil (D) are also shown. DP on day 0 indicates the initial content determined after 1 h of soil flooding. Values represent means \pm SE ($n = 4$). Asterisks in (A) and (B) show significant differences (one-way ANOVA; $p < 0.05$) to rubber and oil palm soils at a given sampling time.

plantations had a more or less stable available P content after an increase ($p < 0.05$) in the first week of flooding (Fig. 2). The same pattern was observed in the subsoil of all land-use types; the subsoil showed an increase in available P only after one week and then stabilized until the last day of flooding.

The effect of land-use type on DP production was similar to that on $D\text{Fe}^{2+}$ production (forest > jungle rubber > oil palm > rubber) throughout the flooding period. DP release started one week after soil flooding (Fig. 3), at the same time when Fe^{3+} reduction and $D\text{Fe}^{2+}$ production also started (Fig. 1). In all land-use types, the DP rates in the topsoil were highest 4 days after flooding (Fig. 3). The land-use influence on DP production was evident in the early stage of flooding (Table A.1). The topsoil of forest showed the highest ($p < 0.05$) DP concentration ($1.61 \text{ mg P kg}^{-1} \pm 0.13$) of all land-use types. DP production ceased 26 days after soil flooding, after which constant values were recorded (Fig. 3). A different trend was observed in the monoculture plantation in both topsoil and subsoil. DP increased only after 7 days of soil flooding with a peak of 6.0 mg P kg^{-1} and 5.0 mg P kg^{-1} in topsoil and subsoil, respectively, and it remained stable thereafter (Fig. 3).

3.3. Changes of Fe-bound phosphorus (Fe-P)

The Fe-P (Fig. 4), which was determined by NaOH-extractable P, clearly decreased after flooding. The maximum decrease of about 50% ($p < 0.05$) was observed in the third week, at about the time when maximum P was liberated. The highest P released ($p < 0.05$) in the topsoil versus subsoil in all land-use types (Fig. 3) corresponds to the Fe-P content (Fig. 4) in the initial state of soil flooding; less Fe-P was

present ($p < 0.05$) in the subsoil than in the corresponding topsoil, and thus the P release in subsoil was less ($p < 0.05$) than in topsoil throughout the flooding period. Nevertheless, a sharp decline ($p < 0.05$) in available P and DP after one month caused the Fe-P content to increase towards its initial level.

3.4. Changes of DOC and soil solution pH

Soil flooding also influenced the DOC concentration (Fig. 5). DOC ($p < 0.05$) was highest in the topsoil of both forest and jungle rubber during the early stage of flooding. This reflects the high SOM content under forest and jungle rubber compared to plantation soils (Table 1). This also explains the 10 times higher DOC ($p < 0.05$) in the topsoil versus subsoil in all land-use types throughout the flooding period.

The soil solution pH declined in the first flooding week (Fig. A.1). Afterwards, it marginally increased (average of 1 unit) in all soils until 45 days and then started to decline again. The trend was similar in both topsoil and subsoil of all land-use types. These results suggested that, in flooded acidic soils, pH will increase and stabilize at a new level after an initial decline. Consequently, this pH change appears to be one of the prerequisites for the solubilization and release of adsorbed P.

4. Discussion

Our data confirmed the results of the previous investigations that soil flooding mobilizes P and increases P availability (e.g., Ponnampuruma, 1972). Interestingly, we found two distinct and opposite phases occurred upon flooding which were not found in the

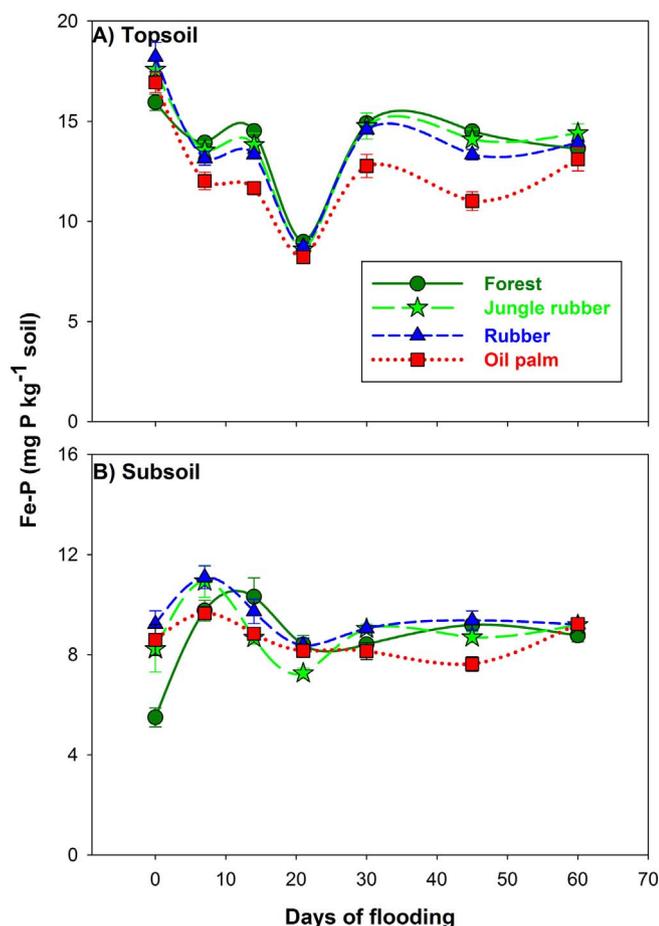


Fig. 4. Effects of soil flooding on the Fe-bound P (P_{NaOH}) of topsoil (A) and subsoil (B) under forest, jungle rubber, rubber and oil palm plantations. Fe-P on day 0 indicates the initial content before soil flooding. Values represent means \pm SE ($n = 4$).

previous investigations. In the first phase during the first three weeks (with maximal intensity in the first week), DFe^{2+} , DP and DOC accumulated in the soil solution (Figs. 1, 3 and 5, respectively). In parallel, the P availability in soil increased, as indicated by a decrease in Fe-P (Fig. 4) and an increase in available-P (Fig. 2). This shows that the impacts of flooding are fast and not limited to P release; rather, soil P forms were also modified to more available fractions. Microbially-mediated reductive dissolution of Fe^{3+} oxides was important during the first three weeks of flooding, as indicated by the significant increase of DFe^{2+} during this period. The similar trend of Fe^{2+} and P release in the soil solution (Figs. 1 and 3, respectively) and the decrease of Fe-P (Fig. 4) confirmed that the reduction and dissolution of Fe(hydr)oxides releases their adsorbed or occluded phosphate (Rakotoson et al., 2015). Our results are in line with the findings of Ponnampereuma (1985), who reported that soil flooding resulted in a decline of Fe-P content and an increase of DP as a result of Fe^{3+} reduction, hydrolysis and dissolution of Fe-P in flooded soil. The increase of the available P fraction in soil suggests that part of the Fe-P affected by iron oxide reduction was not directly released in the soil solution but remained adsorbed on soil particles in a form available for plants, thus reducing potential P losses through leaching.

The Fe-P pool is the main source from which P is released during reduction (Loeb et al., 2008; Zhang et al., 2003). This reduction is influenced by flooding duration. Despite the sharp increase of DFe^{2+} (Fig. 1) during the first three weeks, a significant DP (Fig. 3) release occurred mainly in the first week (except under forest, where a slight

but significant accumulation lasted two additional weeks). Accordingly, Fe^{3+} oxides with high Fe-P content were exhausted after a week of flooding, and the subsequent microbially-mediated reductive dissolution of Fe^{3+} oxides occurred on Fe^{3+} oxides with lower Fe-P content. It is also possible that a larger fraction of Fe-P affected by the reduction of Fe^{3+} oxides in a later stage of flooding was not released as DP but contributed to the more available soil P pool.

Land-use types influenced the impacts of flooding on P and Fe forms mainly in the topsoil, where P dissolution and availability were generally higher under forest and, to a lesser extent, under jungle rubber. Faster solubility in topsoil and especially under forest is connected with a higher C content there (Guillaume et al., 2015), leading to faster microbial consumption of O_2 and consequently faster and more intensive Fe^{3+} to Fe^{2+} reduction. Land-use type effects were not related to initial differences in P or Fe forms because the differences in P and Fe forms were generally much bigger after three weeks of flooding than the initial differences. This indicates that process intensities during flooding were affected by land-use type. The different P concentration between land-use types (Fig. 3) released after soil flooding is explained by the amount of SOM influencing microorganisms. SOM is used as a source of C and energy by the microorganisms and stimulates the microbially-mediated reductive dissolution of Fe^{3+} minerals (Rakotoson et al., 2015; Scalenghe et al., 2002; Zhang et al., 1994). The presence of high native SOM in forest and jungle topsoil drove Fe^{3+} reductions and increased the reduction intensity. Indeed, we recorded a positive relationship ($R^2 = 0.42$; $p < 0.01$; Table 2) between DFe^{2+} and DOC of the topsoil during early flooding. Furthermore, the high DOC in forest and jungle rubber (Fig. 5) highlighted an efficient Fe^{3+} reduction and high release of sorbed P in both forest and jungle rubber topsoil compared to rubber and oil palm soil. Nonetheless, it remains unclear whether DOC was a source of C for microorganisms, thereby enhancing Fe^{3+} reduction, or whether it was a by-product of SOM decomposition during Fe^{3+} reduction, thereby being an indicator of the microbially-mediated reductive dissolution of Fe^{3+} minerals. The direct effect of the low SOM in subsoil in all land-use types resulted to a smaller release of P and Fe compared to topsoil. In conclusion, the extent of microbially-mediated Fe^{3+} reduction was apparently limited by C availability, as observed in other studies (Loeb et al., 2008; Rakotoson et al., 2014, 2015). Accordingly, land-use types affected P mobilization and availability under flooding conditions mostly because forest conversion to plantations strongly decreased SOM.

Part of the P release may originate from mineralization of P bound in SOM, especially during lengthier flooding. Microbial decomposition of SOM to scavenge organic C as an energy source for Fe^{3+} reduction was accompanied by the mineralization of organic P. Several studies have hypothesized that organic P mineralization from SOM is mainly driven by the microorganisms' need for C as their energy (e.g., Achat et al., 2012; Spohn and Kuzyakov, 2013). This hypothesis was verified in the topsoil of all those land-use types with high SOM concentrations, strengthening the land-use effects on P release. This was supported by a strong correlation between available P and DOC ($R^2 = 0.58$; $p < 0.001$; Table 2) and between DP and DOC ($R^2 = 0.56$; $p < 0.001$; Table 2) in the topsoil of all land-use types during early flooding. Nonetheless, the doubling of the DOC concentration in forest between the second and third week of flooding was not followed by the same increase in DP, indicating that DP accumulation was also triggered by factors beyond an accumulation of organic P bound to DOC or released from SOM.

The increasing soil solution pH in topsoil and subsoil across all land-use types may also have influenced the release of P over time. Most reduction reactions consume H^+ , increasing the pH in acid soils; e.g., $Fe(OH)_3 + 3H^+ + e \rightarrow Fe^{2+} + H_2O$ (Narteh and Sahrawat, 1999; Ponnampereuma, 1972). The neutralization of soil pH as a result of

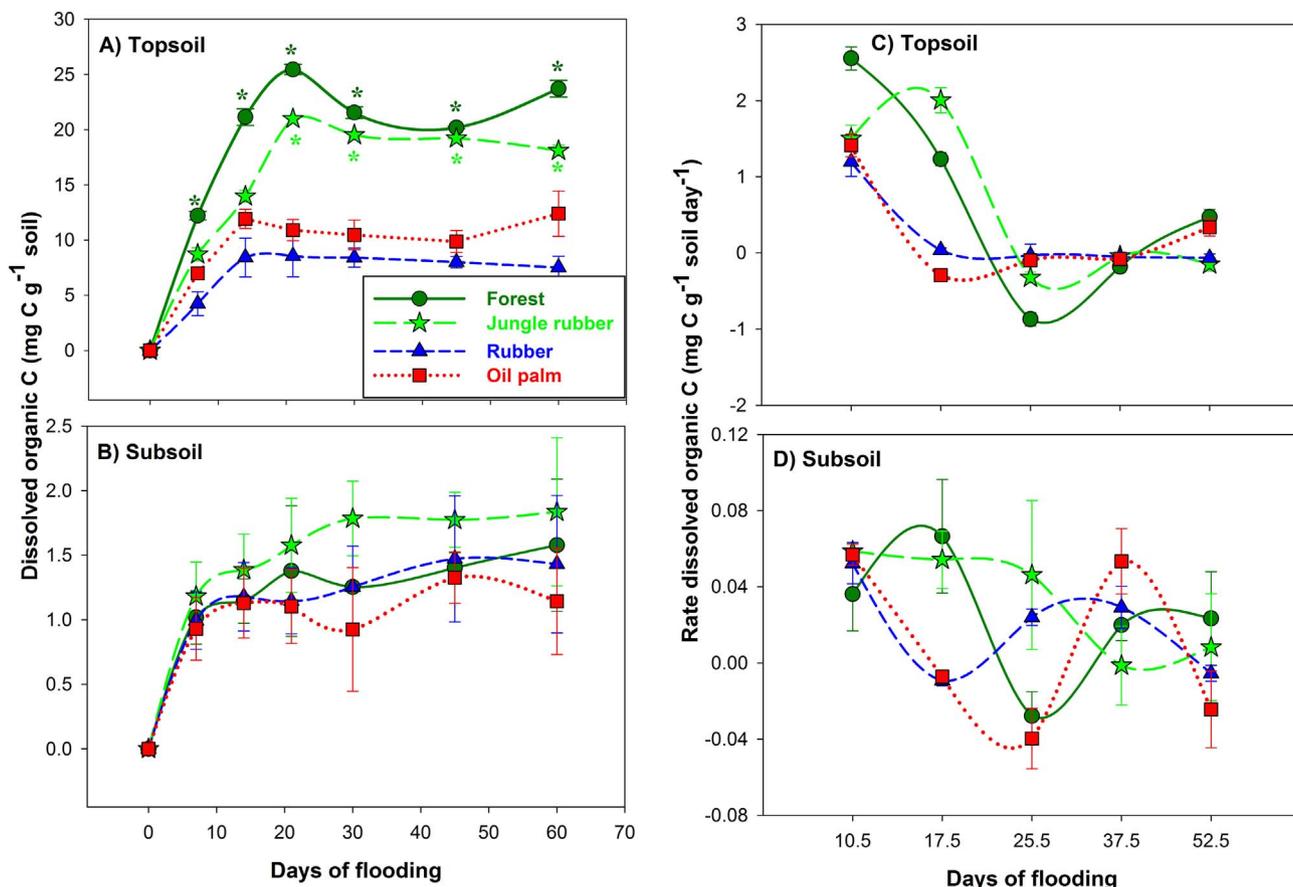


Fig. 5. Effects of soil flooding on DOC under forest, jungle rubber, rubber and oil palm plantations. We compared the DOC of the topsoil (A) and subsoil (B). The computed rates of DOC production in the topsoil (C) and subsoil (D) are also shown. Values represent means \pm SE (n = 4). Asterisks in (A) and (B) show significant differences (one-way ANOVA; $p < 0.05$) to rubber and oil palm soils at a given sampling time.

Table 2
Correlation coefficient (R^2) between concentrations of P forms and associated soil attributes after 21 days (maximum P release) of soil flooding.

	DOC	DFe ²⁺
Avail-P		
Surface	0.58***	0.53**
Subsoil	0.29 ^{ns}	0.08 ^{ns}
DP		
Surface	0.56***	0.38*
Subsoil	0.18 ^{ns}	0.13 ^{ns}
DOC		
Surface	—	0.42**
Subsoil	—	0.10 ^{ns}

ns = not significant; — not applicable.

*** $p < 0.001$.

** $p < 0.01$.

* $p < 0.05$.

reduction processes during flooding increases the solubility of Fe- and Al-P compounds and the desorption of surface P in acid soils (Ponnamperuma, 1972). According to Kashem and Singh (2001), soil pH will approach neutrality (6.5 to 7.5) regardless of the initial value before flooding. In our experiments, soil pH increased with flooding time. However, the first week of flooding caused a pH to decline (Fig. A.1). This was due to the accumulation of CO₂ produced by respiration of aerobic bacteria (Ponnamperuma, 1972) and the influence of continuous production of organic acids because forest and jungle soils contain abundant SOM. The lower pH of forest and jungle topsoil throughout the incubation period was due to the buffering effect of SOM that were abundant in both soils compared to plantation soils.

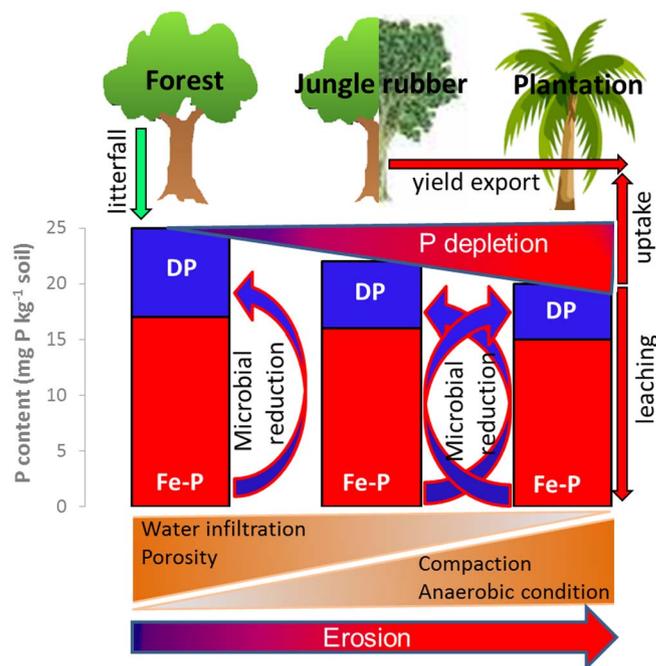


Fig. 6. Conceptual figure showing that reducing conditions mobilize bound P through microbially-mediated Fe reduction and P dissolution making P available for plant uptake. In plantations, anaerobic conditions are more frequent and longer: this increases P availability, accelerates the P cycling, and increased the P uptake by vegetation. Three important P losses are responsible for P depletion: (1) biomass export with yield; (2) soil runoff/erosion and (3) P leaching if the vegetation cannot pump it because of fewer roots in deep soils or less active roots because of anaerobic conditions.

Nonetheless, the influence of soil pH on P release was likely low because pH increased only after one week, when most P was already released.

Long-term incubation showed that iron dissolution and P mobilization were reversible processes. In the second phase, after three weeks, P availability in soils decreased, although Fe-P (Fig. 4) and available P (Fig. 2) did not reach initial levels. The decrease of $D\text{Fe}^{2+}$ (Fig. 1) indicates that microbial reduction of Fe^{3+} eventually stopped or was strongly reduced and that the produced Fe^{2+} underwent secondary chemical reactions, which lead to the precipitation of Fe^{2+} . Our results confirmed the findings of Wood et al. (2015), in which soil solution P increase after flooding is only temporary and restricted to the early reducing conditions, after which it decreased again. We hypothesized that some of the P released via Fe^{3+} reduction would be re-adsorbed to freshly precipitated Fe^{2+} oxides because of their larger adsorptive surface area per unit soil volume (Chacon et al., 2006; Wright et al., 2001). This process, however, was not significant because DP did not decrease following Fe^{2+} precipitation. We were unable to identify the exact cause of changes in Fe^{3+} reduction and P availability, but it was not related to changes in soil pH. One potential explanation is an exhaustion of easily available C sources for microbial reduction. Indeed, DOC concentrations (Fig. 5) decreased in a pattern similar to $D\text{Fe}^{2+}$ concentrations (Fig. 1). In conclusion, even if the increase of available P fractions in soils after flooding is fast but reversible, the P released during initial flooding is not, as long as flooding lasts. Finally, the second phase might only rarely occur in natural conditions because 1) water movements would prevent the establishment of the physico-chemical conditions favoring precipitation and 2) C input by rhizodeposition would prevent C limitation of the microbially-mediated reductive dissolution of Fe^{3+} minerals.

4.1. Ecological relevance

In most tropical soils, P is widely believed to limit plant growth (Cleveland et al., 2006; Townsend et al., 2002; Vitousek, 1984). This is both because of the relatively low total soil P concentrations and because the high Fe and Al oxide content causes a strong fixation of plant available inorganic P into forms unavailable for biota (Bucher et al., 2001; Holford, 1997; Maranguit et al., 2017). Microbially-mediated Fe^{3+} reduction and the associated P release during anaerobic conditions play a fundamental role in the nutrition of plants and microorganisms by releasing inaccessible P during dry conditions. This mechanism is relevant not only in riparian areas or paddy soils, where flooding occurs, but also in well-drained soil partly waterlogged by regular heavy rainfalls during the wet season.

Surprisingly, intensive rubber and oil palm plantations were already strongly depleted in their most refractory P pool a decade after forest conversion and despite P fertilization (Maranguit et al., 2017). This unexpected fast effect of land-use changes on the presumably least reactive P fractions could be driven by a synergy between increased P mobilization by microbially-mediated Fe^{3+} reduction and a higher P output. On one hand, rubber and especially oil palm plantations suffer from soil compaction, resulting in higher bulk density and lower water infiltration and leading to strong erosion (Guillaume et al., 2016; Merten et al., 2016). Consequently, these intensive plantations are more subject to waterlogging and lengthier anaerobic conditions than are more porous soils (e.g., forest and jungle rubber); this makes the cycle turnover of P availability faster (Fig. 6). On the other hand, mobilized P can be exported from the site through runoff/erosion in the plantation. Indeed, strong soil erosion was estimated under rubber and oil palm plantations (Guillaume et al., 2015). Another very important output of mobilized P is through harvested biomass or leaching in groundwater if

the P sink capacity of Fe^{3+} oxide in the subsoil is reduced due to Fe^{3+} reduction. Oil palms have a dense rooting system down to 30 cm depth, but fewer roots than forest in deep soils (Kotowska et al., 2015; Nelson et al., 2006). Hence, oil palms might be less efficient than forest in pumping P mobilized during waterlogged conditions in deep soil, leading to P losses (Fig. 6).

5. Conclusions

The increase of available P and DP during flooding is due to three main mechanisms that were strongly influenced by land-use types: (1) P release via the microbially-mediated reductive dissolution of Fe^{3+} oxides; (2) P release during SOM mineralization and (3) solubility of Fe phosphate due to increasing pH.

Fe^{3+} reduction and P release were pronounced in topsoil compared to subsoil and always higher in forest and jungle rubber than in monoculture plantations throughout the flooding period. The maximum increase of P concentration was in the early stages of flooding, simultaneously with peak $D\text{Fe}^{2+}$ and DOC in the soil solution. The increase of available P and DP in the topsoil of forest and jungle rubber was about 50–70% of the initial concentration before flooding. Consequently, flooding contributed to P mobilization and thus to its potential uptake by plant roots. Fe^{3+} reduction by microorganisms was the key process behind the P release. Nonetheless, the extent of the microbially-mediated reductive dissolution of ferric oxides was apparently determined by the SOM content because it is a source of C and energy that enables microorganisms to efficiently reduce Fe^{3+} . Hence, soils from forest and jungle rubber, which contains high SOM, resulted in a faster and higher P release than the plantation soils. Apart from being an energy source for microorganisms, the mineralization of SOM also contributes to the increase of available P. The P release was higher only in the early stage of flooding across all land-uses and depths. The increasing pH in topsoil and subsoil after flooding of all land-use types also influence the P release. After three weeks of flooding, both P availability in soils and $D\text{Fe}^{2+}$ decreased. This indicates that microbial Fe^{3+} reduction stopped or was strongly reduced and that the Fe^{2+} produced underwent secondary chemical reactions, leading to the precipitation of Fe^{2+} . Nonetheless, the short-term P release via Fe^{3+} reduction provided an important source of available P in flooded ecosystems and in well-drained, highly weathered soil partly waterlogged after seasonal flooding. Anaerobic conditions occur more often in compacted plantation soils compared to forest, and so, the increase P availability under plantations. This accelerates the P cycling: more P is pumped by the vegetation. Three important P losses are responsible for P depletion: (1) soil runoff/erosion; (2) biomass export from yield and (3) P leaching.

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Appendix A

Table A.1

Influence of land-use on the change in DP, DFe²⁺ and DOC of topsoil between two time points as indicated by the p-value of significance evaluated using a repeated measures ANOVA model.

Time	Dissolved P			Dissolved Fe ²⁺			Dissolved org C		
	LU ^a	Δtime ^b	LU * Δtime ^c	LU	Δtime	LU * Δtime	LU	Δtime	LU * Δtime
0	–	–	–	–	–	–	–	–	–
7	0.108 ^{ns}	0.000 ^{***}	0.212 ^{ns}	0.498 ^{ns}	0.000 ^{***}	0.488 ^{ns}	–	–	–
14	0.041 [*]	0.978 ^{ns}	0.001 ^{***}	0.295 ^{ns}	0.000 ^{***}	0.352 ^{ns}	0.000 ^{***}	0.000 ^{***}	0.059 ^{ns}
21	0.009 ^{**}	0.024 [*]	0.085 ^{ns}	0.000 ^{***}	0.032 [*]	0.604 ^{ns}	0.000 ^{***}	0.000 ^{***}	0.000 ^{***}
30	0.012 [*]	0.009 ^{**}	0.015 [*]	0.037 [*]	0.053 ^{ns}	0.952 ^{ns}	0.000 ^{***}	0.006 ^{**}	0.042 [*]
45	0.009 ^{**}	0.531 ^{ns}	0.447 ^{ns}	0.254 ^{ns}	0.017 [*]	0.993 ^{ns}	0.000 ^{***}	0.126 ^{ns}	0.791 ^{ns}
60	0.018 [*]	0.596 ^{ns}	0.651 ^{ns}	0.559 ^{ns}	0.002 ^{**}	0.240 ^{ns}	0.000 ^{***}	0.130 ^{ns}	0.089 ^{ns}

^a p-Value within land-use effect.

^b p-Value of the changes between two time points (e.g., between day 0 and 7; corresponding p-value indicated on day 7).

^c p-Value of the influence of land-use on the change of parameters between two time points.

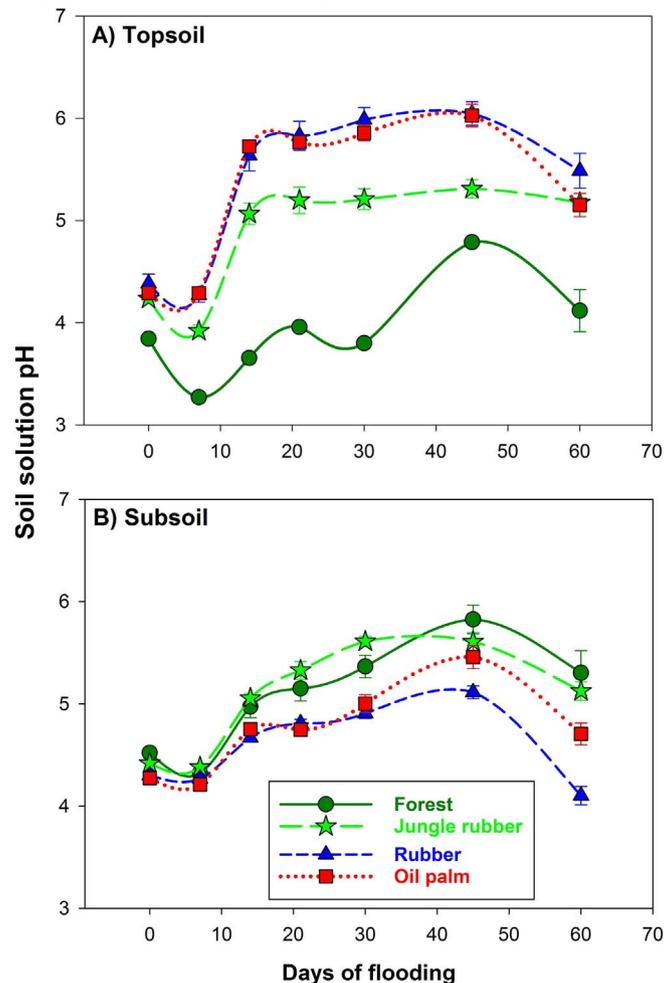


Fig. A.1. Effects of soil flooding on soil pH of topsoil (A) and subsoil (B) under forest, jungle rubber, rubber and oil palm plantations. pH on day 0 indicates initial value before soil flooding. Values represent means \pm SE (n = 4).

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