

Phosphorus uptake of rice plants is affected by phosphorus forms and physicochemical properties of tropical weathered soils

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Abstract

Aims Phosphorus (P) deficiency is a major constraint for rice production in the tropics. Field-specific P management is key for resource-limited farmers to increase yields with minimal inputs. We used soil P fractionation analysis to identify the relevant factors controlling P uptake and the responses to P fertilization of rice in flooded and highly weathered soils.

Methods Phytometric pot-based experiments and a modified Hedley fractionation analysis were repeated for soils from extensive regions and from geographical adjacent fields in Madagascar.

Results Large field-to-field variations in indigenous P supply from soils (total P uptake of rice when P is

omitted) and fertilizer-P recovery efficiencies (increased P uptake when P is applied) were observed not only for soils with various geological backgrounds but also for soils from adjacent fields. Regression models indicated that the indigenous P supply in soils was largely controlled by readily available inorganic and organic P pools ($r^2 = 0.72$), whereas fertilizer-P recovery efficiencies were controlled by the abundance of oxalate-extractable aluminum and iron in soils ($r^2 = 0.81$).

Conclusions Spatial heterogeneity even within adjacent fields leads to benefits from field-specific fertilizer management based on indigenous P supply from soils and fertilizer-P recovery efficiencies evaluated by different soil properties.

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Keywords Hedley fractionation · Nutrient omission trial · Phosphorus uptake · Rice · Sub-Saharan Africa

Abbreviations

| | |
|-------------------|--|
| Alo | oxalate-extractable Al |
| ANOVA | Analysis Of Variance |
| Δ Biomass | the difference in biomass of rice plant between the +NP and +N treatments |
| Feo | oxalate-extractable Fe |
| ICP | Inductively Coupled Plasma |
| P _i | inorganic P in each fraction |
| P _o | organic P in each fraction |
| P _{i+o} | total P in each fraction |
| Δ P uptake | the difference in P uptake of rice plant between the +NP and +N treatments |
| SSA | Sub-Saharan Africa |
| TEB | Total Exchangeable Bases |

Introduction

Reduced availability of phosphorus (P) in soils results in reduced biomass and grain yield of rice grown in highly weathered soils (Dogbe et al. 2015; Fageria and Baligar 1997; Koné et al. 2011, 2013). Therefore, improvement of P availability in tropical weathered soils and enhancement of P uptake in rice plants is crucial to meet the rising demand for rice in Sub-Saharan Africa (SSA) (Nziguheba et al. 2016; Saito et al. 2015b; van Oort et al. 2015). Tropical weathered soils are typically acidic and rich in iron (Fe) and aluminum (Al) (hydr)oxides, which result in a substantial capacity to sorb phosphate (Balemi and Negisho 2012). These features may partly explain why the increase of P availability due to the reduced condition is less expected in highly weathered soils, while P availability generally tends to be less-limiting for paddy rice than for upland crops in equivalent soils (Fageria et al. 2011). There is also concern regarding the non-renewable use of global rock-phosphate reserves (Van Vuuren et al. 2010), and fertilization is usually neither economical nor readily available to subsistence farmers in SSA (Nziguheba et al. 2016). Hence, under such circumstances, it is necessary for farmers to adopt strategies to improve the P uptake of rice plants, through 1) selecting a field with a high indigenous P supply capacity, and/or 2) increasing fertilizer-P recovery efficiency.

In rice fields, in which soil fertility varies spatially, site-specific soil management is expected to benefit rice

production (Saito et al. 2015a; Schmitter et al. 2010; Yanai et al. 2012). This may be particularly true for the fields of smallholder farmers in SSA, where the response to applied nutrients varies over small distances and is governed mostly by the influence of past management practices (Kihara et al. 2016; Schut et al. 2018; Zingore et al. 2011). In addition, our previous studies indicated that the forms of soil P were important for determining P availability in the tropics and that soil P forms can be affected by land management practices as well as soil properties (Nishigaki et al. 2018; Sugihara et al. 2012). Therefore, it is necessary to evaluate the spatial variation of soil P forms in rice fields on a regional or community scale and to elucidate the response of P uptake in rice to the P forms in soils.

The P fractionation method of Hedley et al. (1982) has been widely used to characterize soil P forms based on their availability, with the fundamental assumption being that extractants of varying strength estimate P fractions of differing availability. Nevertheless, P fractions separated by the same sequential method are not of equal availability to plants in all soils (Guo et al. 2000), and rice plants draw P from a continuum of chemically extracted fractions that are assumed to have different plant P availability (Zhang et al. 2006). In low-input systems, in which fertilizer-P additions are very low or absent, pools of P that are less available seem to act as a buffering pool for labile inorganic P, particularly in highly weathered soils (Beck and Sanchez 1994; Guo et al. 2000). In addition, previous studies argued that organic P may play an important role in supplying available P in unfertilized soils (George et al. 2018; Guo et al. 2000; Tiessen et al. 1992). However, little is known about the significance of these different P pools in the supply of P to rice plants grown on weathered soils.

The focus for low-P soils in the tropics is on increasing fertilizer-P recovery efficiency and preventing the accumulation of recalcitrant soil P (Menezes-Blackburn et al. 2017). In the normal pH range of agricultural soils of the tropics, P is mainly bound to Fe- and Al-(hydr)oxides, with the sorption reactions including the precipitation of metal phosphates (Haynes and Mokolobate 2001). Alternatively, it is widely reported that soluble organic constituents derived from the application of organic amendments can enhance P solubility and mobility, as well as compete with P for sorption sites

(Chassé and Ohno 2016; Guppy et al. 2005; Yan et al. 2013). It is, therefore, necessary to take into account not only the soil P forms, but also other soil physicochemical properties that inhibit or enhance P absorption by rice plants. Thus far, few studies have shown how rice P uptake is regulated by soil P forms and soil physicochemical properties in highly weathered soils.

Relative biomass or nutrient uptake (ratio with the omission of a target nutrient relative to its full application) has been used in previous omission trials as an index to evaluate nutrient deficiency (Kihara et al. 2016; Shehu et al. 2018). Still, there are debates about this index and whether it can clearly identify the influential factors with respect to high P-fixing capacity, the originally high P-supplying capacity, and deficiencies of other nutrients. In this study, we aimed to distinguish the indigenous soil P-supplying capacity and the fertilizer-P recovery efficiency using different parameters, i.e., total P uptake of rice plants in the P-omitted treatment and increased P uptake with P application, respectively. Our objective was, therefore, to evaluate P uptake of rice plants with special reference to soil P forms and soil physicochemical properties in tropical weathered soils. Of particular interest was to examine the variations in P forms in a range of rice-field soils and to determine the factors that have a substantial effect on P uptake in rice plants.

Materials and methods

Soil sampling and pot-based experiments

Two sets of pot-based experiments were conducted with lowland and upland field soils collected from a wide region of the central highland of Madagascar ($n = 35$, Exp. 1) and those collected within a relatively small area of one village ($n = 16$, Exp. 2) (Fig. 1). These two sets of experiments were to confirm the applicability of the results at the landscape level in soils that have been rather affected by geological changes and at the field-scale level in soils rather affected by individual farmers' management practices. Experimental soils were taken from 0 to 15 cm depth as composites of four to five cores in each field and divided into two parts for the pot-based experiments and soil analysis, respectively. Each of Exp. 1 and Exp. 2 was conducted in a greenhouse at the Laboratoire des Radio-Isotopes, University of Antananarivo, in Madagascar (18°53'56.0"S, 47°33'01.2"E, 1222 m alt.) during September to October 2016 (Exp. 1) and December 2016 to

January 2017 (Exp. 2). The daily mean temperatures throughout the growing periods ranged from 18.2 to 25.6 °C and from 21.6 to 25.9 °C in Exp. 1 and Exp. 2, respectively (Watchdog 2475, Spectrum Technologies Ltd.).

Each of the collected soils was put into a 1-l plastic pot (13 cm diameter, 15 cm height). Each pot contained 1 kg of air-dried and sieved (4 mm) soil. In each experiment, three sets of different fertilizer treatments were established with two replicates: 1, *Cont* (no fertilizer application); 2, +*N* (0.2 g pot⁻¹ and 0.3 g pot⁻¹ of N as NH₄NO₃ in Exp. 1 and Exp. 2, respectively); 3, +*NP* (0.2 g pot⁻¹ and 0.3 g pot⁻¹ of both N as NH₄NO₃ and P₂O₅ as KH₂PO₄ in Exp. 1 and Exp. 2, respectively). Potassium was applied to all the pots, including the *Cont* treatment at the rate of 0.2 g pot⁻¹ and 0.3 g pot⁻¹ of K₂O as KCl in Exp. 1 and Exp. 2, respectively. Each nutrient was uniformly incorporated into soils one day after being flooded and one day prior to transplanting. Then, two 20-day-old seedlings of a local rice cultivar, X265, grown in free-nutrient sand were transplanted to each pot. The pots were continuously flooded at the depth of 2–5 cm with distilled water throughout the growing periods. The weeds were removed manually, and no specific pest management was required.

Plant analysis

The plants were harvested at the soil surface, 34 days after transplanting for both Exp. 1 and Exp. 2. Above-ground biomass was determined after oven drying at 70 °C to a constant weight. Each plant sample was ground into a fine powder using a high-speed vibrating sample mill (Model T1–100, Heiko Co. Ltd., Fukushima, Japan). Then, the plant P concentration was determined with the molybdate blue method (Murphy and Riley 1962) after dry-ashing at 550 °C for 2 h and digestion with 0.5 M HCl. The plant P uptake (mg P pot⁻¹) was calculated as the product of aboveground biomass and P concentration of plants (total P content).

Soil analysis

The collected soils were air-dried and sieved to 2 mm for subsequent soil analysis. Soil particle size distribution was determined with the wet-sieving and pipet method (Gee and Bauder 1986). Soil pH was determined in deionized water at a soil-to-solution ratio of 1:2.5. Exchangeable cations (K⁺, Na⁺, Ca²⁺, and Mg²⁺) were

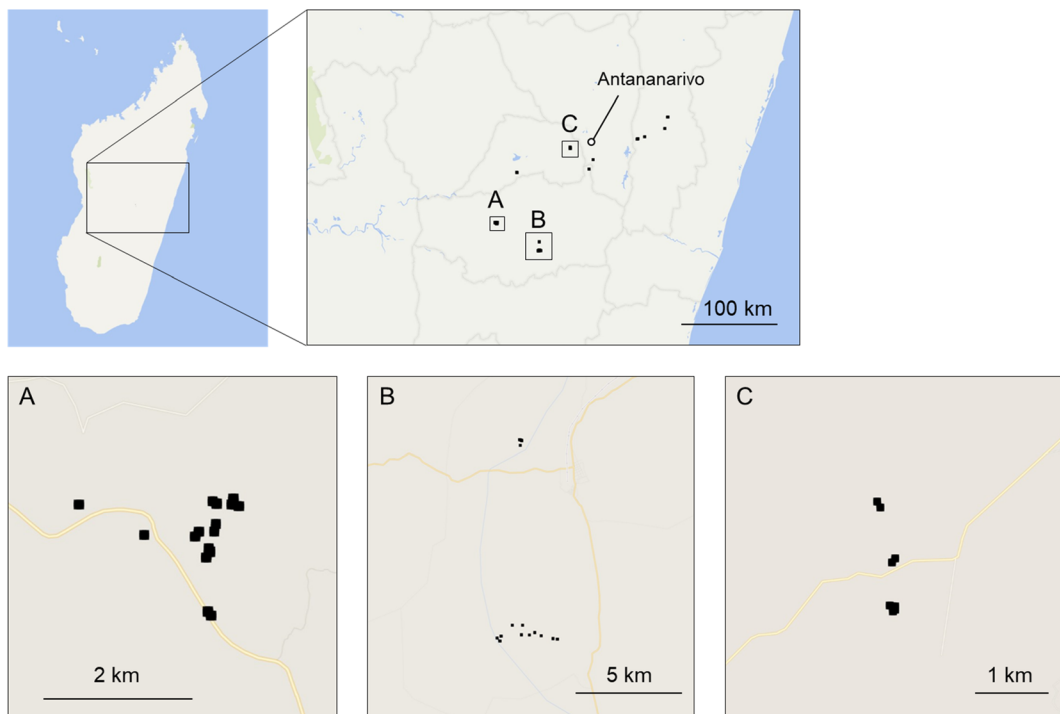


Fig. 1 Map of soil sampling sites. Soils for Exp. 2 were collected from the sites in sub-map A, whereas soils for Exp. 1 were from the other sites

measured following ISRIC protocol (2002), and total exchangeable base was calculated as the sum of those four cations. Total carbon (C) and N were quantified using the dry combustion method with an NC analyzer (Sumigraph NC-220F, SCAS, Japan). Soil samples were digested in 60% HClO₄ following Kuo (1996), and total P was determined with the molybdovanadate method (Kitson and Mellon 1944). Extractable Al, Fe, and P contents were determined with the acid ammonium oxalate method (Alo, Feo, and Oxalate P, respectively) as described by Courchesne and Turmel (2008). The concentrations of Al, Fe, and P in the oxalate extraction were measured with an inductively coupled plasma mass spectrometer (ICPE-9000, Shimadzu, Japan).

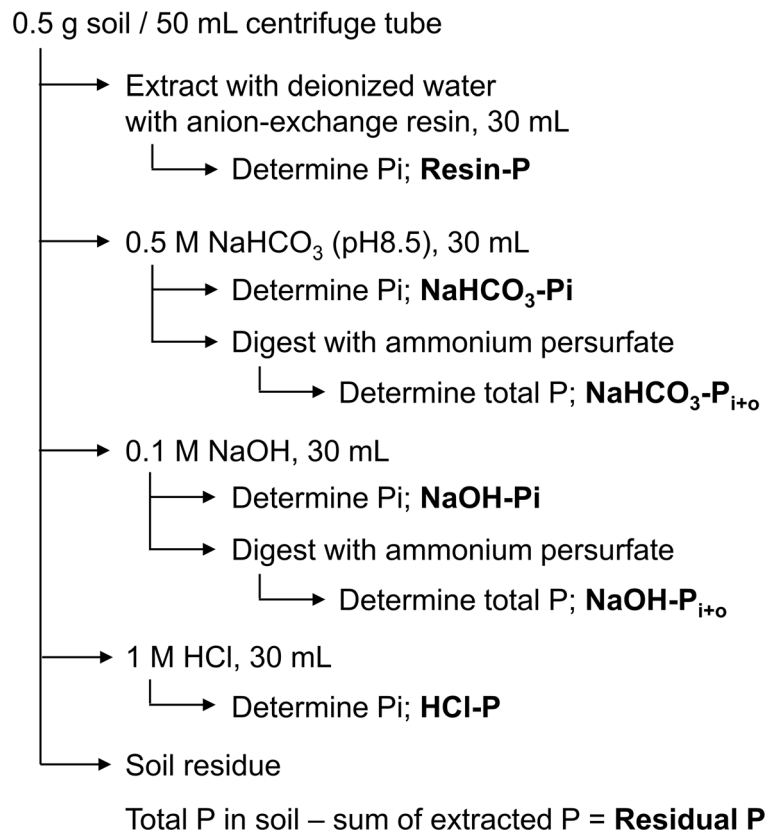
Soil P was sequentially fractionated using a modification of the Hedley method (Tiessen and Moir 2007; Sugihara et al. 2012) (Fig. 2). Briefly, 0.5 g of soil was placed in a 50 mL centrifuge tube and sequentially extracted with 30 mL of each of the extractant solutions, which were added in the following order: deionized water (deionized water with two anion-exchange resins in the bicarbonate form; Resin-P), 0.5 M NaHCO₃ (pH 8.5) (NaHCO₃-P), 0.1 M NaOH (NaOH-P), and 1 M HCl (HCl-P). Each extraction was performed for 16 h using a horizontal shaker followed by centrifugation at 2500×g for

20 min at room temperature, and the supernatant was filtered (5C, ADVANTEC) and the filtrate collected to measure the concentration of inorganic P (Pi) using the molybdate-ascorbic acid method (Murphy and Riley 1962) after pH adjustment using *p*-nitrophenol. Each total P (P_{i+o}) in NaHCO₃ and NaOH extracts was determined after digestion with ammonium persulfate in an autoclave at 103.5 kPa and 120 °C for 60 min, and the concentration was determined with the method of Murphy and Riley (1962). The organic P (Po) was calculated as the difference between P_{i+o} and Pi. The difference between total P in soils and the sum of Pi and Po in all the extracted fractions was defined as Residual P.

Statistics

Statistical analyses were performed using JMP11 software (JMP11.0 Windows, SAS Institute Inc.). First, two-way analysis of variance (ANOVA) was conducted to determine the individual and interaction effects of soils (S) and fertilizer treatments (T) on the above-ground biomass and total P uptake of rice plants. Second, the obtained above-ground biomass and total P uptake data for both Exp. 1 and Exp. 2 were standardized into the mean value at 0 with the sample variation at

Fig. 2 Simple flow chart of the sequential P extraction according to a modified Hedley method (Tiessen and Moir 2007; Sugihara et al. 2012)



1 to simultaneously handle the results of two experiments grown under different environmental conditions. Then, a stepwise regression analysis was repeated by applying the K-fold ($K = 5$) cross validation to develop robust models over two experiments that explained the variations in: 1) total P uptake in the $+N$ treatment as an index of indigenous soil P-supplying capacity, and 2) differences in P uptake between the $+N$ and $+NP$ treatments as an index of fertilizer-P recovery efficiency, respectively. The candidate explanatory factors included clay content, total C, N, and P contents, soil pH, A_{10} , Fe_0 , $A_{10} + 0.5 Fe_0$, Resin-P, $NaHCO_3$ -Pi, $NaHCO_3$ -Po, NaOH-Pi, NaOH-Po, and HCl-P. In the stepwise process, the ‘selection’ and ‘removal’ of factors was controlled with an F-value of $P < 0.10$ at each step. The step ended when no remaining candidate factors produced an eligible F-value. Then, a multiple linear regression model was developed using the selected variables. At the end, standardized partial regression coefficients were calculated to assess the effect size of each selected variable. In addition, a *t*-test for the simple regression coefficient was conducted to identify the interrelationship of these soil properties.

Results

Plant biomass and P uptake

Compared with Exp. 1, Exp. 2 yielded higher values for both aboveground biomass and total P uptake; this was attributable to the higher temperature and rate of nutrient application as well as greater amount of solar radiation during the growing period (Table 1). ANOVA demonstrated highly significant effects of experimental soil, fertilizer treatment, and most importantly of their interactions on aboveground biomass and P uptake for both Exps. 1 and 2. Consequently, there were large variations in biomass and P uptake within each experiment. In a comparison of F-values, the magnitude of variations as affected by different soils and treatments was almost equivalent between the two experiments even though the soils for Exp. 2 were collected from adjacent fields in a small area of one village.

The aboveground biomass in the $+N$ treatment ranged from 0.20 to 2.01 g pot^{-1} and 1.38 to 6.40 g pot^{-1} in Exp. 1 and Exp. 2, respectively (Fig. 3a). The effect of P application, as measured by the difference in biomass between the $+NP$ and $+N$ treatments (Δ Biomass), was

Table 1 Aboveground biomass and P uptake of rice plants as affected by different soils and fertilizer treatments

| | | Aboveground biomass (g pot ⁻¹) | | | Plant P uptake (mg P pot ⁻¹) | | |
|---------------|---------------|--|-------|----------|--|--------|-----------|
| | | mean | s.d. | | mean | s.d. | |
| Exp. 1 | Cont | 0.48 c | 0.33 | | 0.63 b | 0.69 | |
| | +N | 0.75 b | 0.48 | | 0.81 b | 0.80 | |
| | +NP | 1.89 a | 0.57 | | 3.29 a | 1.34 | |
| Exp. 2 | Cont | 1.36 c | 0.53 | | 1.89 c | 1.78 | |
| | +N | 3.37 b | 1.25 | | 3.20 b | 2.84 | |
| | +NP | 5.60 a | 0.64 | | 10.36 a | 3.59 | |
| ANOVA summary | | Aboveground biomass | | | Plant P uptake | | |
| | | df | SS | F-value | df | SS | F-value |
| Exp. 1 | Soil (S) | 35 | 26.1 | 12.5*** | 16 | 134.2 | 14.6*** |
| | Treatment (T) | 2 | 66.7 | 556.7*** | 2 | 283.4 | 538.6*** |
| | S × T | 70 | 14.1 | 3.4*** | 32 | 69.8 | 3.8*** |
| Exp. 2 | Soil (S) | 16 | 31.9 | 8.7*** | 16 | 428.1 | 43.5*** |
| | Treatment (T) | 2 | 296.3 | 645.9*** | 2 | 1275.3 | 1036.2*** |
| | S × T | 32 | 23 | 3.1*** | 32 | 108.3 | 5.5*** |

Mean values with different letters indicate significant differences based on Tukey HSD at $P < 0.05$

s.d., standard deviation ($n = 35$ and $n = 16$ for Exp. 1 and Exp. 2, respectively); df, degrees of freedom; SS, sum of squares

*** $P < 0.001$

positive for all soils whereas the increased rate varied greatly among soils, ranging from 0.08 to 2.33 g pot⁻¹ (Exp. 1) and from 0.40 to 4.72 g pot⁻¹ (Exp. 2). The same soil-to-soil or field-to-field variations were observed for the P uptake data in the +N treatment, and P uptake increased when P was applied (Fig. 3b). The P uptake without P application (+N treatment) ranged from 0.10 to 2.77 mg P pot⁻¹ (Exp. 1) and 0.95 to 12.97 mg P pot⁻¹ (Exp. 2). The increased P uptake when P was applied (ΔP uptake; difference between the +NP and +N treatments) ranged from 0.47 to 5.02 mg P pot⁻¹ (Exp. 1) and from 2.67 to 10.14 mg P pot⁻¹ (Exp. 2). Interestingly, there were large differences in the response to P application, i.e., Δ Biomass and ΔP uptake, even among the

soils that consistently had low biomass production or P uptake under +N treatment (P omitted).

Soil characteristics, total P and fractionated P

The original soils in Exp. 2 had poor nutrient status in terms of total C, N, and P compared with the soils in Exp. 1 (Table 2). Because the soils for Exp. 2 were collected from a small area within a single community, the standard deviation values for most soil properties were smaller in Exp. 2 than Exp. 1. The Alo and Alo + 0.5 Feo values were significantly greater for the soils of Exp. 1 than those of Exp. 2, whereas Feo was comparable between the experiments.

Fig. 3 Biomass (a) and P uptake (b) in the +N treatment and their responses to P application. Δ Biomass, the difference in biomass of rice plant between the +NP and +N treatments; ΔP uptake, the difference in P uptake of rice plant between the +NP and +N treatments

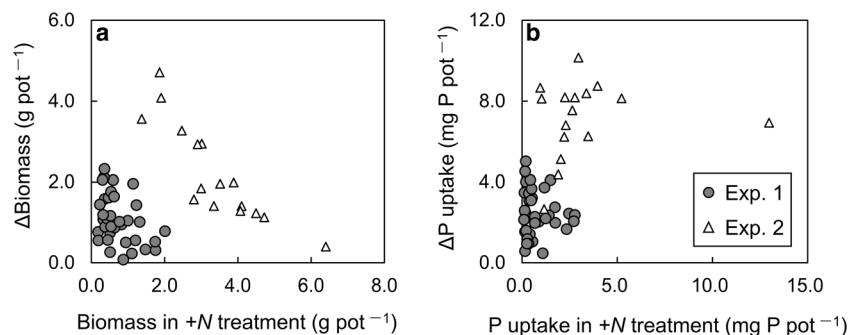


Table 2 Physicochemical properties of soils for pot-based experiments

| | | Exp. 1 | | | Exp. 2 | | | Total | |
|-----------------------|---------------------------------------|----------|---|--------|----------|---|--------|----------|--------|
| | | (n = 35) | | | (n = 16) | | | (n = 51) | |
| Total C | (g C kg ⁻¹) | 26 | a | (11.0) | 14 | b | (5.2) | 22 | (11.1) |
| Total N | (g N kg ⁻¹) | 2.0 | a | (0.8) | 1.2 | b | (0.4) | 1.7 | (0.8) |
| Total P | (mg P kg ⁻¹) | 1200 | a | (720) | 540 | b | (190) | 960 | (670) |
| TEB | (cmol _c kg ⁻¹) | 3.4 | | (3.2) | 2.8 | | (2.4) | 3.2 | (3.0) |
| pH (H ₂ O) | | 5.6 | | (0.4) | 5.6 | | (0.3) | 5.6 | (0.4) |
| Clay | (%) | 32 | | (8.2) | 31 | | (10.5) | 32 | (9.0) |
| Alo | (g Al kg ⁻¹) | 4.3 | a | (2.6) | 1.4 | b | (0.5) | 3.4 | (2.6) |
| Feo | (g Fe kg ⁻¹) | 8.6 | | (5.0) | 5.8 | | (4.2) | 7.7 | (5.0) |
| Alo + 0.5 Feo | (g kg ⁻¹) | 8.6 | a | (4.5) | 4.3 | b | (1.8) | 7.2 | (4.3) |

The values given in parentheses are standard deviation. Different letters indicate a significant difference between the experiments (Tukey test, $P < 0.05$)

TEB, total exchangeable bases (sum of exchangeable Ca²⁺, Mg²⁺, Na⁺, and K⁺); Alo, oxalate-extractable Al; Feo, oxalate-extractable Fe

Total P concentration in all soils ranged from 200 to 3200 mg P kg⁻¹, with a mean value of 960 mg P kg⁻¹ (Fig. 4). The amount of P varied substantially among the fractions, with the NaOH-Pi value being greatest (260 mg P kg⁻¹ on average) followed by NaOH-Po (81 mg P kg⁻¹ on average). The HCl-P was generally low in most soils (median 8.0 mg P kg⁻¹), but some soils had quite high HCl-P values that increased with soil pH. The Resin-P, NaHCO₃-Pi, and NaHCO₃-Po values were lower than for the other fractions, namely 12, 19, and 18 mg P kg soil⁻¹ on average, respectively. The Oxalate P in all soils ranged from 49 to 1200 mg P kg soil⁻¹ (mean, 330 mg P kg soil⁻¹). The ratio of the sum of labile P (Resin-P, NaHCO₃-Pi, and NaHCO₃-Po) to total P was smaller in Exp. 2 (4.9%) than Exp. 1 (6.1%). Except for

the NaHCO₃-Po fraction, all fractions had a significant positive correlation with total P (Table 3).

The Alo values correlated significantly with Resin-P, NaHCO₃-Pi, and NaOH-Pi, whereas the Feo values correlated only relatively weakly in this respect (Table 3). The Alo + 0.5 Feo values also correlated significantly with Resin-P, NaHCO₃-Pi, and NaOH-Pi (Table 3). The amount of Oxalate P clearly corresponded to the total amount of extractable Pi in all the fractions (TPi) (Fig. 5).

Relationship between responses to fertilizer application and soil properties

Table 4 presents the results of step-wise regression analysis for P uptake in the +N treatment and for the

Fig. 4 Variation of total phosphorus and fractionated phosphorus among soil samples (n = 51). The cross in each box represents the mean, the central vertical bar shows the median, the box represents the interquartile range, the whiskers show the location of the most extreme data points that are still within a factor of 1.5 of the upper or lower quartiles, and the points are values that fall outside the whiskers

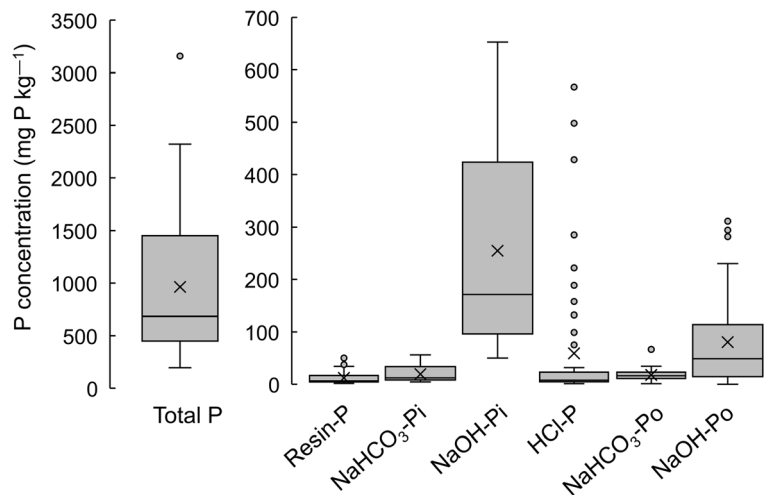


Table 3 Correlation matrix among soil physicochemical properties and fractionated phosphorus

| | Total P | Oxalate P | Resin-P | NaHCO ₃ -Pi | NaOH-Pi | HCl-P | TPi | NaHCO ₃ -Po | NaOH-Po | TPo | Residual P |
|------------------------|----------|-----------|----------|------------------------|----------|----------|----------|------------------------|----------|----------|------------|
| Alo | 0.703 ** | 0.764 ** | 0.619 ** | 0.719 ** | 0.857 ** | 0.438 | 0.783 ** | 0.494 | 0.714 ** | 0.724 ** | 0.476 |
| Feo | 0.552 * | 0.700 ** | 0.463 | 0.599 ** | 0.502 | 0.496 | 0.572 * | -0.059 | 0.425 | 0.305 | 0.473 |
| Alo + 0.5Feo | 0.733 ** | 0.854 ** | 0.632 ** | 0.769 ** | 0.796 ** | 0.544 * | 0.792 ** | 0.259 | 0.655 ** | 0.604 ** | 0.553 * |
| pH (H ₂ O) | 0.374 | 0.456 | 0.342 | 0.357 | 0.201 | 0.618 ** | 0.418 | -0.447 | -0.093 | -0.090 | 0.368 |
| Clay | -0.145 | -0.256 | -0.246 | -0.188 | -0.071 | -0.413 | -0.237 | 0.284 | 0.121 | 0.139 | -0.106 |
| Total C | 0.367 | 0.351 | 0.227 | 0.385 | 0.603 ** | -0.049 | 0.387 | 0.536 * | 0.765 ** | 0.766 | 0.172 |
| Total P | 1.000 ** | 0.874 ** | 0.782 ** | 0.894 ** | 0.864 ** | 0.742 ** | 0.930 ** | 0.189 | 0.604 ** | 0.575 * | 0.939 ** |
| Oxalate P | | 1.000 ** | 0.890 ** | 0.915 ** | 0.823 ** | 0.837 ** | 0.950 ** | 0.194 | 0.478 | 0.439 | 0.724 ** |
| Resin-P | | | 1.000 ** | 0.888 ** | 0.780 ** | 0.772 ** | 0.898 ** | 0.251 | 0.331 | 0.309 | 0.628 ** |
| NaHCO ₃ -Pi | | | | 1.000 ** | 0.907 ** | 0.710 ** | 0.953 ** | 0.276 | 0.567 * | 0.503 | 0.743 ** |
| NaOH-Pi | | | | | 1.000 ** | 0.510 | 0.919 ** | 0.498 | 0.727 ** | 0.704 ** | 0.666 ** |
| HCl-P | | | | | | 1.000 ** | 0.807 ** | -0.130 | 0.097 | 0.060 | 0.689 ** |
| TPi | | | | | | | 1.000 ** | 0.282 | 0.542 ** | 0.505 | 0.770 ** |
| NaHCO ₃ -Po | | | | | | | | 1.000 ** | 0.371 | 0.468 | 0.003 |
| NaOH-Po | | | | | | | | | 1.000 ** | 0.994 ** | 0.425 |
| TPo | | | | | | | | | | 1.000 ** | 0.403 |
| Residual P | | | | | | | | | | | 1.000 ** |

Alo, oxalate-extractable Al; Feo, oxalate-extractable Fe; Oxalate P, oxalate-extractable P; TPi, sum of extracted inorganic P; TPo, sum of extracted organic P; Residual P, difference between total P in soils and the sum of inorganic and organic P in all the extracted fractions

* $P < 0.01$, ** $P < 0.001$

difference in P uptake (ΔP uptake) between the +N and +NP treatments using various soil properties. The Resin-P and NaHCO₃-Po were selected as the positive explanatory variables for P uptake in the +N treatment, whereas Alo and total P were selected as negative explanatory variables. Using these selected parameters, the regression model explained 72% of the variation in P uptake of the +N treatment across Exp. 1 and Exp. 2. The standardized partial regression coefficients indicated that the effect size of selected variables decreased in the order of Resin-P, Alo, NaHCO₃-Po, and total P. Using the same procedure, Alo + 0.5 Feo was selected as a strong and negative explanatory variable for ΔP uptake. In addition, total C was selected as a weak and negative explanatory variable ($P = 0.051$). The multiple linear regression analysis of these two variables

explained 81% of the variation in ΔP uptake across Exp. 1 and Exp. 2.

Discussion

Large field-to-field variations in soil P status and response of rice to nutrient inputs

Two sets of pot-based experiments confirmed that the production of irrigated rice—at least in the early growth stage—is limited by P deficiency in most of the soils in the central highland of Madagascar. In addition, there were large field-to-field variations in responses of rice production or P uptake when P was omitted (+N treatment) and when P was applied (+NP treatment)x

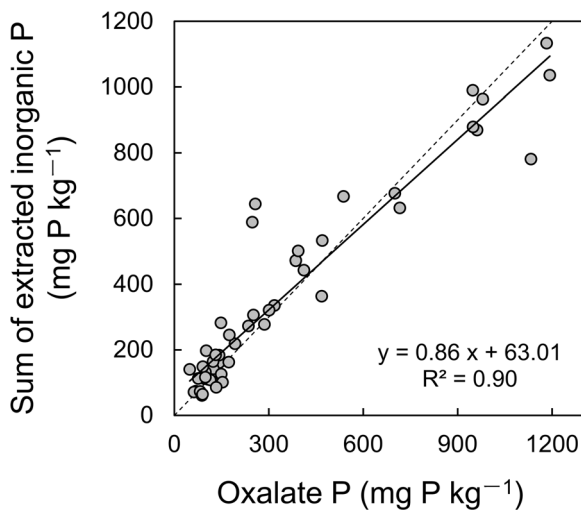


Fig. 5 Relationship between oxalate-extractable P and sum of extracted inorganic P. **footer:** Solid line shows best fit from regression analysis, and the broken line shows 1:1 ratio

(Table 1, Fig. 3); these large variations in the indigenous soil P-supplying capacity and fertilizer-P recovery efficiencies were confirmed not only for those soils differing in geological backgrounds within a particular region (Exp. 1) but also for soils in adjacent fields in a small area (Exp. 2) (Table 1). The results corroborate recent assertion that better information is needed concerning

Table 4 Multiple regression analysis for plant P uptake in the +N treatment and difference in P uptake between the +NP and +N treatments

| | Selected variable | Partial regression coefficient | Standardized partial regression coefficient |
|--------------------------|--------------------------|--------------------------------|---|
| P uptake in +N treatment | Intercept | -1.170 ^{ns} | -0.471 ^{ns} |
| | Resin-P | 0.034 ^{***} | 0.419 ^{***} |
| | NaHCO ₃ -Po | 0.021 ^{***} | 0.222 ^{***} |
| | Alo | -0.100 ^{***} | -0.286 ^{***} |
| | Total P | -0.0003 [*] | 0.197 [*] |
| | Adjusted R square = 0.72 | | |
| ΔP uptake ^a | Intercept | 1.010 ^{ns} | 0.252 ^{ns} |
| | Alo + 0.5 Feo | -0.056 ^{**} | -0.244 ^{**} |
| | Total C | -0.158 [†] | -0.177 [†] |
| | Adjusted R square = 0.81 | | |

^a Difference in phosphorus uptake between +NP and +N treatments

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † $P = 0.051$; ns, not significant

Alo, oxalate-extractable Al; Feo, oxalate-extractable Fe

differences in the response to applied nutrients within and between fields to effectively increase yields and returns of inputs for smallholder farmers in SSA (e.g. Schut et al. 2018).

Phosphorus is generally considered to have less mobility compared with other plant nutrients because of its strong fixation to the high levels of Fe and Al oxides in tropical soils. Therefore, soil P status is relatively consistent within a geological background at the landscape level (Nishigaki et al. 2018). However, our results for soil P index revealed a substantial variation in total P and fractionated P despite the inclusion of samples collected over small distances. Total P was generally high in the lowland soils compared with the soils collected from adjacent upland fields supposedly due to the replenishment of sediments in runoff water in the lowland fields. Yet, large variations in total P were observed even within lowland soils in a small area (see [Supplementary data sheet](#)). Schmitter et al. (2010) also reported a large spatial variation in soil physicochemical properties in rice paddy terraces in Northwest Vietnam. These results support the importance of site-specific fertilizer management practices based on differences in soil P status and responses of rice to P fertilizer. The large variation in soil P status that we observed in Madagascar could be attributable to land management practices and pervasive soil erosion on the sloping topography.

P uptake of rice plants in relation to soil P supply capacity

The result of the regression analysis revealed that P uptake of rice without P application was increased by Resin-P and NaHCO₃-Po, indicating that these fractions constitute a readily available P pool in soils for rice grown under flooded conditions (Table 4). In other words, the indigenous P supply for lowland rice largely relies on Resin-P, which accounts for merely 1% of total P in soils (Fig. 4). In addition, our results revealed a quantitative effect of labile organic P (NaHCO₃-Po) on the P uptake values of rice plants in highly weathered soils. Indeed, previous studies have emphasized the potential role of organic P pool as a source of available P in tropical weathered soils (George et al. 2018; Turner 2006).

The total organic P pool (NaHCO₃-Po and NaOH-Po) in this study was 97 mg P kg⁻¹, representing 10% of total P. This is comparable with results of a previous report on soil organic P in rice fields in Madagascar, i.e., the Po pool ranged from 6.7% to 29% (Turner 2006).

Randriamanantsoa et al. (2015) reported that gross organic P mineralization rates were 0.8 ± 0.5 mg P $\text{kg}^{-1} \text{day}^{-1}$ and 1.7 ± 0.2 mg P $\text{kg}^{-1} \text{day}^{-1}$ in non-amended and residue-amended Ferralsols, respectively. Our results and those of these previous studies also support the potential role for soil organic P in rice nutrition at the initial growth stage in tropical soils that typically have low available inorganic P. On the other hand, Alo in soils had a negative effect on P uptake of rice. This is likely attributable to the high sorption capacity of active Al in soils (Agbenin 2003; Nwoke et al. 2003). We therefore conclude that the P-supplying capacity of strongly weathered rice-fields is mainly controlled by the size of the labile inorganic and organic P pools and the sorption capacity of the soil matrix. However, the potential contribution of less-labile P fractions through the root-induced chemical reactions in rhizosphere soils (Hinsinger 2001) should not be completely excluded when we consider relatively low P mobility in highly weathered soils and the mass balance between P uptakes of rice plants and labile P pools in rhizosphere soils.

Effect of oxalate-extractable Al, Fe, and P on fertilizer-P recovery efficiency and P cycling

The result of the regression analysis revealed that the difference in P uptake between the +NP and +N treatments was strongly controlled by the Alo + 0.5 Feo (Table 4). This underscores the importance of Al and Fe (hydr)oxides in regulating fertilizer-P recovery efficiency for lowland rice production in highly weathered soils. This suggests that the applied P was mainly sorbed to the active Al and Fe, and hence P availability for plants decreased. Sugihara et al. (2012) reported that P in fertilizer was predominantly fixed by Al and Fe oxides in a clay-rich maize cropland in Tanzania. Nwoke et al. (2003) also suggested that oxalate-extractable Al and Fe can regulate the standard P requirement and P availability in soils of the West African savanna.

We found that the Alo + 0.5 Feo correlated positively with each inorganic P fraction, and most highly with $\text{NaHCO}_3\text{-Pi}$ and NaOH-Pi , suggesting that P in these labile and less-labile fractions is mainly associated with the active Al and Fe. Despite the large proportion of NaOH-Pi in total P (Fig. 4), NaOH-Pi did not contribute to the P uptake of rice in +N treatment owing to the low availability of P strongly fixed by the active Al and Fe. Considering the higher regression coefficients for Alo

than Feo with $\text{NaHCO}_3\text{-Pi}$ and NaOH-Pi , Alo is likely to be the main controlling factor for those fractions. Nwoke et al. (2003) suggested that Al plays a greater role than Fe in removing P from soil solution of the surface layer because the pH values of soils are in the range in which P is more likely to react with Al than with Fe.

It has been reported that the application of organic matter, such as animal manure, can decrease P sorption and increase P availability in highly weathered soils (Azeez and Averbeke 2011; Guppy et al. 2005), owing to competition between organic matter molecules and P for the available sorbing sites on soil particles (Chassé and Ohno 2016). Hence, farmyard manure application, which is widely used for agricultural lands in the central highlands of Madagascar, is indeed an effective management option for improving the phytoavailability of applied phosphate in weathered soils. Andriamananjara et al. (2018) reported that farmyard manure application to weathered upland soils of Madagascar increases P fertilizer recovery efficiency for upland rice.

Our results reveal that the amount of Oxalate P clearly corresponded to sum of extracted inorganic P (Fig. 5). This fact leads us to surmise that Oxalate P represents all the labile and less-labile inorganic P pools in soils. Most of the P sorbed by active Fe and Al compounds is slowly released back to the soil solution, providing service flows for 5 to 10 years (Sanchez et al. 1997). Agbenin and Goladi (1998) indicated that Resin-P is attributable to the less-labile P sources, namely NaOH-Pi and HCl-P , which act as sinks for fertilizer-P. These results suggest that Oxalate P can be an index for the evaluation of both labile and less-labile P pools, namely the moderately active P pool, which may be involved in the subsequent slow P cycling in rice croplands (Lookman et al. 1995). This could account for why many previous studies, which were mostly conducted using soils with an abundant labile P pool, have shown that Oxalate P is poorly effective at predicting P uptake by crops (Eichler-Löbermann et al. 2007; Nawara et al. 2017). Interestingly, however, we found a significant correlation between P uptake and Oxalate P in both Exp. 1 ($r=0.75$, $P<0.001$ in the *Cont* treatment) and Exp. 2 ($r=0.72$, $P<0.01$ in the *Cont* treatment). This is likely attributable to the fact that less-labile P in tropical weathered soils is more abundant than in temperate soils and, therefore, the overall effect of less-labile P is greater in tropical weathered soils.

Conclusion

Our experiments successfully extracted the most relevant soil components to determine the indigenous soil P-supplying capacity and fertilizer-P recovery efficiencies for rice production. Phosphorus uptake of rice in the early growth stage is tightly controlled by labile inorganic and organic P pools and active Al and Fe in P-deficient weathered soils. In addition, a high degree of variability in rice P uptake in response to fertilizer treatment and soil characteristics is observed even within a small area. These results provide fundamental information for developing more effective nutrient management practices and improving financial returns for individual fields. Further studies are required to determine whether the results from our pot-based experiments are applicable to the responses of rice in the field. To achieve practical field-specific fertilizer management, further studies are also needed to reveal how to increase available P—in both inorganic and organic forms—and to reduce the activity of Al and Fe oxides in highly weathered soils.

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