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Biological P cycling is influenced by the form of P fertilizer in an Oxisol

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Abstract Phosphate rock (PR) is an alternative fertilizer to increase the P content of P-deficient weathered soils. We evaluated the effects of fertilizer form on indicators of biological cycling of P using an on-farm trial on a Rhodic Kandiudox in western Kenya. Treatment plots were sampled after 13 cropping seasons of P applications as Minjingu phosphate rock (PR) or as triple super phosphate (TSP) (50 kg P ha⁻¹ season⁻¹), as well as a P-unfertilized control (0 kg P ha⁻¹ season⁻¹). Soils (0–15 and 15–30 cm) were analyzed for microbial biomass P (Pmic), activities of acid phosphomonoesterase, alkaline phosphomonoesterase, and phosphodiesterase, and sequentially extractable P fractions. P additions as Minjingu PR yielded 299% greater P_{mic} than TSP at 0-15cm depth despite similar labile P concentrations in the two P fertilization treatments and stimulated activities of acid phosphomonoesterase (+39%). When added in the soluble form of TSP, a greater percentage of total soil P was present in mineral-bound forms (+33% Fe- and Al-associated P). Higher soil pH under Minjingu PR (pH 5.35) versus TSP (pH 5.02) and the P-unfertilized treatment (pH 4.69) at 0-15-cm depth reflected a liming effect of Minjingu PR. The

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form of P fertilizer can influence biological P cycling in weathered soils, potentially improving P availability under Minjingu PR relative to TSP via enhanced microbial biomass P and enzymatic drivers of P cycling.

Keywords Phosphorus · Phosphatase · Microbial biomass phosphorus · Oxisol · Phosphate rock · Kenya · Permanganate-oxidizable carbon

Introduction

Phosphorus (P) deficiency remains a key constraint to agricultural productivity in weathered soils of sub-Saharan Africa (Nziguheba et al. 2016). Ameliorating P deficiency can be accomplished by recapitalizing soils with P inputs (Buresh et al. 1996; Sanchez et al. 1997). Acidulated P fertilizers such as triple super phosphate (TSP) offer soluble and rapidly available P, but access and affordability limit their use by smallholder farmers (Jama and Kiwia 2009; Nziguheba et al. 2016). In many parts of sub-Saharan Africa, phosphate rock deposits are an economical alternative to TSP (Jama and Van Straaten 2006; Nandwa and Bekunda 1998). The largest high-quality deposit of PR (10⁷ t) in East Africa is Minjingu phosphate rock (PR) (Van Kauwenbergh 1991; van Straaten 2002). Though less soluble than TSP, Minjingu PR exhibits sufficient dissolution in acid, P-deficient soils to secure comparable or greater improvement of yields in the medium-term (>3 years) (Szilas et al. 2007b). However, it is not known how P fertilization in the form of Minjingu PR versus TSP may affect biological cycling of soil P, which in weathered soils is considered key to plant availability and could therefore modulate long-term response to P recapitalization strategies.

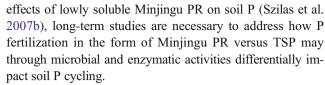
Soil microbial biomass and phosphatases are known to influence soil P availability in acid, weathered soils (Ayaga



et al. 2006; Cui et al. 2015; Marschner 2008). Microbial biomass can serve as a reservoir of available P because microbial immobilization of soil solution P avoids its geochemical capture (Oehl et al. 2001), and subsequent turnover of microbial biomass enables scavenged P to become transiently available to plants (Achat et al. 2010; Oberson and Joner 2005). Soil phosphatases are a class of enzymes that catalyze the mineralization of organic P (P_o) into plant-available inorganic P (P_i), and their activity is generally stimulated under conditions of P limitation (Nannipieri et al. 2011). Soil P_o diester forms are first hydrolyzed by phosphodiesterases, with subsequent hydrolysis of resulting monoester P_o forms to P_i by acid and alkaline phosphomonoesterases (Tabatabai 1994; Turner and Haygarth 2005).

P inputs to agroecosystems are known to impact soil microbial biomass P (Pmic) and phosphatase activities, but the potential response of these biological drivers of P cycling to the form of P fertilizer type (e.g., phosphate rock versus TSP) remains unknown. Since microbial biomass can rapidly incorporate labile P (Bünemann et al. 2004c), additions of soluble P fertilizers such as TSP can increase Pmic in weathered soils (Gichangi et al. 2010; Malik et al. 2012). On the other hand, a 5-year field experiment in western Kenya found that P_{mic} was not influenced by fertilization with TSP (50 kg P ha⁻¹ year⁻¹) (Bünemann et al. 2004a). Characterization of phosphatase activities in weathered soils under cultivation in East Africa is limited to a few studies and mostly acid phosphomonoesterase activity (Bossio et al. 2005; Mukuralinda et al. 2011; Radersma and Grierson 2004; Verchot and Borelli 2005). Despite the suppression of expression of phosphatases by P_i (Nannipieri et al. 2011), TSP fertilization in weathered soils in this region at low (25 kg P ha⁻¹) and high (250 kg P ha⁻¹) rates did not decrease acid phosphomonoesterase activity (Mukuralinda et al. 2011; Radersma and Grierson 2004). However, it is not known how activities of acid phosphomonoesterase and additional phosphatases that modulate P cycling may be influenced by the form of P fertilizer in these agroecosystems.

Limited evidence suggests that the form of P fertilizer as Minjingu PR or TSP could influence biological P cycling in weathered soils in the short term. For example, within three cropping seasons, application of Minjingu PR to a weathered soil in western Kenya increased the population of P solubilizing bacteria (PSB) by up to 90%, whereas TSP reduced the P-solubilizing bacteria population by 46–69% (Ndungu-Magiroi et al. 2015). Since secretion of extracellular phosphatases is one of the P acquisition strategies employed by P-solubilizing bacteria (Jones and Oburger 2011), Minjingu PR fertilization may have also engendered changes in soil phosphatase activities. However, the response of P_{mic} and phosphatase activities to management strategies was not characterized. Given the short-term instability of soil P dynamics in response to P fertilization in weathered soils (Beck and Sanchez 1994) and lag



We investigated the effect of P fertilizer on indicators of biological P cycling after 13 cropping seasons in an on-farm trial situated on a weathered soil in western Kenya. We evaluated the impact of P fertilization as Minjingu PR on soil $P_{\rm mic}$ and phosphatase activities relative to TSP, contextualized by soil P fractions. We hypothesized that at the same recommended P fertilization rate, Minjingu PR would increase $P_{\rm mic}$ and phosphatase activities relative to TSP.

Methods

Site description and sampling

The on-farm trial was established in 2007 in Sidada, in Siaya County in western Kenya (34°24′E, 00°08′N) by the African Network for Soil Biology and Fertility program (AfNet) and was co-managed by the International Center for Tropical Agriculture (CIAT). The trial is designed to evaluate Minjingu PR and TSP added to maize (Zea mays)-based cropping systems. The region experiences a mean annual temperature of 23 °C and mean annual precipitation of 1800 mm distributed over two rain seasons composed of a short rain period (September-November) and a period of long rain (March-June). The trial is situated on a Rhodic Kandiudox (USDA taxonomy) or Rhodic Acric Ferralsol (WRB taxonomy), with clay texture (578 g clay kg⁻¹, 207 g silt kg⁻¹, 215 g sand kg⁻¹) and pH 5.4 at 0–30 cm depth in an adjacent uncultivated soil profile (Jelinski, unpublished). Further details are provided by Savini et al. (2016).

Two P fertilization treatments were selected to represent Minjingu PR and TSP at 50 kg P ha⁻¹ season⁻¹, a rate recommended for western Kenya (KARI 1994; Kihara and Njoroge 2013). Minjingu PR contained 12.8% total P, 23% of which is considered soluble as per neutral ammonium citrate extraction (Savini et al. 2016). TSP contained 45% P, 90% of which is soluble (Havlin et al. 2013). A P-unfertilized (0 kg P ha⁻¹) treatment was also sampled as a control. Treatment plots (6 m × 6 m) were cropped to maize in the long rains and common bean (Phaseolus vulgaris) in the short rains, with tillage and weeding performed by the farmer using a hand hoe. To highlight effects of P fertilization, all plots received background fertilization of 60 kg potassium (K) ha⁻¹ as muriate of potash and 60 kg nitrogen (N) ha⁻¹ as urea per season. All fertilizers, including P, were added by hand broadcasting as per local practices. After the 13th cropping season and prior to soil preparation for maize planting (e.g., tillage and fertilization), soils for individual treatment plots (n = 3 per



treatment) were sampled by auger as a plot composite (n = 3) at 0–15 and 15–30 cm depths.

General soil properties

Soil pH was measured in deionized water (1:5) after 30 min of equilibration. Soil organic carbon (SOC) was determined with an ECS 4010 CHN Analyzer (Valencia, CA). Permanganate-oxidizable C was determined using the method of Weil et al. (2003) as modified by Culman et al. (2012). Briefly, 2.50 g soil was oxidized with 0.02 M KMnO₄ by 2 min shaking followed by 10-min incubation. Non-reduced permanganate was quantified by colorimetry (550 nm).

Soil P fractions

Soil P distribution was assessed by sequential extraction. Triplicate soil samples (2 g) were sequentially extracted (Hedley et al. 1982; Tiessen and Moir 1993). A negative control (no soil) and soil standard were also included. Anion-exchange membranes (AEM; 1 × 4 cm, VWR International, West Chester, PA) were loaded with carbonate as the counterion. Soils were extracted with AEM in deionized water by shaking for 18 h. Inorganic P (P_i) was desorbed from the membranes by shaking for 3 h in 0.25 M H_2SO_4 . All other extracts were centrifuged (8000×g, 5 min) and an aliquot decanted for analysis. For NaOH aliquots, organic matter was precipitated with 1.2 M H₂SO₄ and the precipitate was separated by centrifugation (8000 $\times g$, 15 min). Aliquots were neutralized and analyzed for P_i and total P (Pt). Inorganic P was estimated by molybdate colorimetry at 880 nm (Murphy and Riley 1962). Total P in aliquots was determined by the same procedure following acid-persulfate digestion (80 °C, 16 h) (Rowland and Haygarth 1997). Organic P (P_o) was estimated as the difference between total and inorganic P (i.e., $P_0 = P_t - P_i$). To simplify interpretation, Hedley fractions were considered to represent labile P (AEM-P_i + NaHCO₃-P_i), Fe- and Alassociated P (NaOH-P_i), Ca-associated P (HCl-P_i), and organic P (NaHCO₃-P_o + NaOH-P_o) (Tiessen et al. 1983; Turrión et al. 2007). Total soil P was estimated independently by ashing (550 °C, 1 h) followed by acid extraction (1 M H₂SO₄, 1:50 soil/extractant, 16 h) and molybdate colorimetry (Dieter et al. 2010).

Microbial biomass P (P_{mic})

 $P_{\rm mic}$ was measured using sequential fumigation-extraction according to Brookes et al. (1982). Briefly, soils were preincubated for 2 weeks at 65% of water-filled pore space (WFPS). For each soil sample (i.e., treatment plot), three types of subsamples were processed: fumigated, non-fumigated, and spiked with P_i . Duplicate soil samples (2 g) were treated

with chloroform gas for 18 h followed by extraction with 40-mL 0.5 M NaHCO₃ (pH 8.5, 1 h). Centrifugation was used to obtain a clear supernatant (8000×g, 15 min), an aliquot of which was used to determine P_i by molybdate colorimetry (Brookes et al. 1982; Murphy and Riley 1962). Nonfumigated and P-spiked subsamples were processed in the same way as fumigated subsamples, but without chloroform fumigation. A P spike (50 μg P g^{-1} soil) was used to estimate P recovery in fumigated samples. P_{mic} was calculated as the difference between fumigated and non-fumigated extractable P and corrected for P spike recovery.

In order to evaluate the relative magnitude of soil P stored in microbial biomass, P_{mic} was expressed as a percent of total soil P. As P_{mic} is considered a potentially plant-available P pool in weathered soils (Ayaga et al. 2006), the ratio of P_{mic} to labile P was calculated to evaluate the relative proportions of these two measures of potentially available P.

Soil phosphatase activities

Acid phosphomonoesterase (Enzyme Commission 3.1.3.2), alkaline phosphomonoesterase (EC 3.1.3.1), and phosphodiesterase (EC 3.1.4.1) activities were assayed as described by Tabatabai (1994), using 1 g of air-dried soil incubated for 1 h at 37 °C in 4-mL modified universal buffer (MUB) at pH 6.5 for acid phosphomonoesterase and at pH 11.0 for alkaline phosphomonoesterase, or in 4-mL 0.05 M Tris (2-amino-2-(hydroxymethyl)-1,3-propanediol) buffer at pH 8.0 for phosphodiesterase. Assays employed a final substrate concentration of 0.01 M para-nitrophenyl phosphate (acid phosphomonoesterase and alkaline phosphomonoesterase) or bispara-nitrophenyl phosphate (phosphodiesterase). A negative control (no soil) and a positive control (lab soil standard) were also included. Reactions were halted by the addition of 4-mL 0.5 M NaOH to acid phosphomonoesterase and alkaline phosphomonoesterase assays or 4-mL 0.1 M Tris (pH 12.0) to phosphodiesterase assays, and 1-mL 0.5 M CaCl₂. Assays were centrifuged (8000 ×g, 4 min) to remove sediment, and para-nitrophenol (pNP) in the clear supernatant was quantified colorimetrically at 410 nm. Absorbance from the negative controls was subtracted from absorbance of soil assays.

Statistical analyses

The effect of P fertilizer form (Minjingu PR vs TSP) on soil properties was evaluated with pairwise *t* tests using Proc TTEST in SAS v.9.4 (Cary Institute, NC). To evaluate the effect of P-fertilization, Dunnett's test was used to compare response of Minjingu PR and TSP relative to the P-unfertilized control using Proc GLM. Comparison of Minjingu PR and TSP (*t* test) is reported in tables, whereas comparisons between Minjingu PR, TSP, and P-unfertilized treatments are reported in the text and/or in a Supplementary



Table. Relationships among soil properties across treatments and depths were evaluated by Pearson correlation analysis using Proc CORR with the correlation coefficient (*R*) and significance (*p* value).

Results

Soil properties

Soil properties showed weak differences between Minjingu PR and TSP after 13 cropping seasons, though P inputs increased soil pH and permanganate-oxidizable C compared to no P fertilization (Table 1, Supplementary Table 1). Soil pH was elevated under Minjingu PR relative to TSP at 0-15 cm depth (p = 0.097). Though permanganate-oxidizable C did not differ by P fertilizer form, Minjingu PR increased SOC (+10%) at 15– 30 cm depth (p = 0.069) compared to TSP, a trend that was weaker at 0–15 cm depth (p = 0.132). Concurrent with elevated SOC, soil C/P_o was greater at 15–30 cm depth under Minjingu PR (C/P_o 226) compared to TSP (C/P_o 209) (p = 0.093), and only under Minjingu PR was significantly elevated relative to the P-unfertilized control (Supplementary Table 1). P fertilization using Minjingu PR but not TSP significantly increased soil pH relative to no P fertilization at both depths (e.g., pH 4.69 vs 5.35 at 0–15 cm, p = 0.025), and P fertilization increased permanganate-oxidizable C by a mean of 35% at 0-15 cm depth (p = 0.0003) (Supplementary Table 1).

Soil P pools

Soil P fractions indicated greater P availability of P added as Minjingu PR than as TSP (Table 2). Minjingu PR yielded 89% greater labile P at 15–30 cm depth compared to TSP

(p=0.040). Concurrent with lower labile P, TSP additions resulted in 33% greater Fe- and Al-associated P at 0–15 cm depth. Organic P and Ca-associated P did not differ between P fertilizers. Though total P was higher under TSP at 0–15 cm depth (p=0.045), there was no difference in total P at 0–30 cm depth by the form of P fertilizer (p=0.25). P fertilization for 13 cropping seasons produced significant increases in P pools at both depths relative to no P fertilization except organic P, which decreased at 0–15 cm depth with P fertilization.

Microbial biomass P (P_{mic})

The form of P fertilizer had a significant effect on P_{mic} at 0–15 cm depth (Fig. 1). Mean P_{mic} was 299% greater under Minjingu PR (23.1 $\mu g~g^{-1}$) than TSP (5.3 $\mu g~g^{-1}$). P_{mic} was significantly elevated under Minjingu PR but not TSP relative to the P-unfertilized control (2.8 $\mu g~g^{-1}$). Additionally, P_{mic} represented a greater percentage of total soil P under Minjingu PR (3.5%) than under TSP (0.8%) at 0–15 cm depth, which was similar to no P fertilization (0.6%) (Fig. 2). The percentage of P_{mic} relative to labile P at 0–15 cm depth was greater under Minjingu PR ($P_{mic}/P_{labile}=0.59$) relative to TSP ($P_{mic}/P_{labile}=0.13$) (Fig. 3).

At 15–30 cm depth, P_{mic} was similar between Minjingu PR (9.4 μg g⁻¹) and TSP (6.8 μg g⁻¹) (Fig. 1) and represented a similar percentage of total and labile P between P fertilizer forms (Fig. 2). At 15–30 cm depth, P fertilization increased P_{mic} by 343% from 1.8 μg g⁻¹ (P-unfertilized) to 8.1 μg g⁻¹ (Minjingu PR, TSP) (Fig. 3). P_{mic} was positively correlated with total and labile P across treatments and depths (e.g., $R_{labile\ P}=0.61,\ p=0.0075$) (Supplementary Table 2). Excluding TSP treatment for 0–15 cm depth revealed a stronger correlation of P_{mic} and labile P ($R=0.91,\ P<0.0001$). P_{mic} was positively correlated with pH ($R=0.46,\ p=0.053$),

Table 1 Soil properties in a Rhodic Kandiudox in western Kenya following 13 cropping seasons of fertilization with Minjingu phosphate rock (PR) or triple super phosphate (TSP)

	pН		$SOC (mg g^{-1})$		$POXC\ (\mu g\ g^{-1})$		C/P _o	
	mean	se	Mean	se	mean	se	mean	se
0–15 cm								
Minjingu PR	5.35	0.08	19.7	0.6	362	15	222	21
TSP	5.02	0.13	18.0	0.6	331	31	179	12
P-unfertilized	4.69	0.08	18.0	0.5	256	16	154	6
p	0.097		0.132		0.388		0.149	
15-30 cm								
Minjingu PR	5.39	0.04	19.0	0.6	279	32	226	5
TSP	5.35	0.13	17.3	0.6	263	12	209	4
P-unfertilized	5.04	0.04	17.3	0.3	255	56	183	8
p	0.790		0.069		0.642		0.093	

Significance (p value) between Minjingu PR and TSP treatments was determined by pairwise t test. A P-unfertilized treatment is included as a reference

se standard error, C/Po ratio of total C to organic P, SOC soil organic C, POXC permanganate-oxidizable C



Table 2 Soil P fractions (μg g⁻¹) in a Rhodic Kandiudox in western Kenya following fertilization with Minjingu phosphate rock (PR) or triple super phosphate (TSP) over 13 cropping seasons

	Labile P		Organic P		Fe-, Al-P		Ca-P		Total P	
	mean	se	mean	se	mean	se	mean	se	mean	se
0–15 cm										
Minjingu PR	38.3	3.2	89.7	6.7	143.9	8.4	3.2	0.3	663.7	9.3
TSP	46.1	2.9	100.5	1.9	191.4	11.3	2.7	0.3	717.2	16.6
P-unfertilized	2.5	0.2	117.3	2.6	63.3	2.9	1.0	0.1	454.6	6.0
P	0.092		0.16		0.004		0.31		0.045	
15–30 cm										
Minjingu PR	15.9	3.0	94.9	11.8	71.1	10.0	1.3	0.1	534.2	30.7
TSP	8.4	1.5	83.0	4.1	67.4	8.7	1.1	0.2	460.3	14.0
P-unfertilized	0.9	0.0	94.9	2.7	26.8	0.8	1.1	0.1	390.1	3.1
P	0.040		0.36		0.79		0.255		0.10	

Labile P is the sum of anion-exchange membrane extractable P_i and sodium bicarbonate extractable P_i , organic P is the sum of sodium bicarbonate extractable P_o and sodium hydroxide extractable P_o , Fe-, and Al-associated P is sodium hydroxide extractable P_i , and Ca-associated P is hydrochloric acid extractable P_i . Significance (p value) between Minjingu PR and TSP treatments was determined by pairwise t test. A P-unfertilized treatment is included as a reference

se standard error, P_i inorganic P, P_o organic P

permanganate-oxidizable C (R = 0.48, p = 0.046) and C/P_o (R = 0.62, p = 0.0062), but not organic P.

Phosphatase activities

Activities of particular soil phosphatases were elevated under P fertilization with Minjingu PR than with TSP (Fig. 4). At 0–

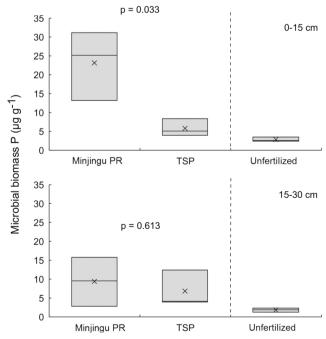


Fig. 1 Soil microbial biomass $P(P_{mic})$ in a Rhodic Kandiudox in western Kenya following 13 cropping seasons of fertilization with Minjingu phosphate rock (PR) or triple super phosphate (TSP) at 50 kg P ha⁻¹ season⁻¹, with a P-unfertilized control as a reference

15 cm depth, acid phosphomonoesterase was 39% greater under Minjingu PR (4.8 μ mol pNP g^{-1} h^{-1}) than under TSP (3.4 μ mol pNP g^{-1} h^{-1}). At 15–30 cm depth, phosphodiesterase was elevated under Minjingu PR (1.8 μ mol pNP g^{-1} h^{-1}) compared to TSP (1.4 μ mol pNP g^{-1} h^{-1}) (p = 0.10). Across depths, activities of acid phosphomonoesterase and alkaline phosphomonoesterase were positively correlated (R = 0.80, p = 0.0017), but only alkaline phosphomonoesterase activity

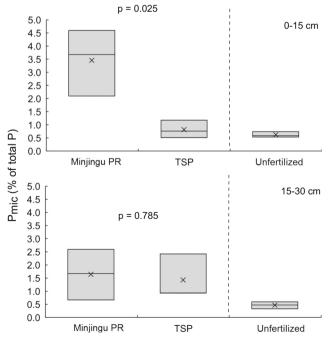


Fig. 2 Soil microbial biomass P (P_{mic}) as a percentage of total soil P following fertilization for 13 cropping seasons with Minjingu phosphate rock (PR) or triple super phosphate (TSP) at 50 kg P ha⁻¹ season⁻¹, with a P-unfertilized control as a reference



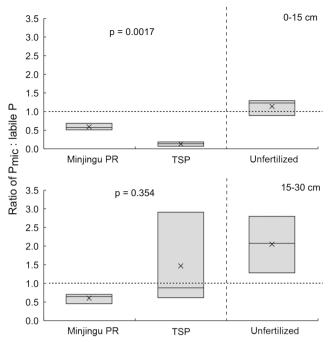


Fig. 3 Proportion of soil microbial biomass P (P_{mic}) relative to labile P (P_{mic} /labile P), following fertilization for 13 cropping seasons with Minjingu phosphate rock (PR) or triple super phosphate (TSP) at 50 kg P ha⁻¹ season⁻¹, with a P-unfertilized control as a reference

was correlated with phosphodiesterase activity (R = 0.64, p = 0.0046) (Supplementary Table 2). Activity of acid

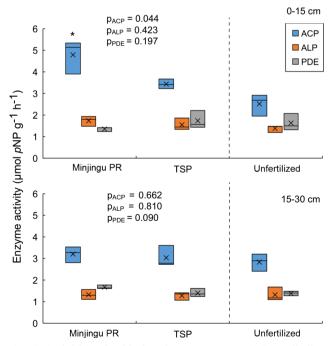


Fig. 4 Activities of acid phosphomonoesterase (ACP), alkaline phosphomonoesterase (ALP), and phosphodiesterase (PDE) determined by *para*-nitrophenol assay in a Rhodic Kandiudox in western Kenya following 13 cropping seasons of fertilization with Minjingu phosphate rock (PR) or triple super phosphate (TSP) at 50 kg P ha⁻¹ season⁻¹, with a P-unfertilized control as a reference

phosphomonoesterase was higher under P fertilization (mean + 80%) relative to no P fertilization at 0–15 cm depth. Phosphatase activities were positively correlated with SOC, labile P, and total P, but not organic P. $P_{\rm mic}$ was correlated with acid phosphomonoesterase (R=0.69, p=0.0015) and alkaline phosphomonoesterase (p=0.039), but not phosphodiesterase (p=0.29) (Supplementary Table 2). Across the pH range encompassed by treatments (pH 4.69–5.35, Table 1), the activity of alkaline phosphomonoesterase and acid phosphomonoesterase but not phosphodiesterase increased with soil pH (e.g., for alkaline phosphomonoesterase R=0.61, p=0.0072), and a similar trend occurred for permanganate-oxidizable C.

Discussion

Increases in microbial biomass P with phosphate rock fertilization

The hypothesized effect of P fertilizer type on microbial biomass P was supported by increases in P_{mic} under Minjingu PR. A greater percentage of total P as P_{mic} under Minjingu PR relative to TSP suggests greater availability of P added as PR. This is consistent with higher Fe- and Al-associated P (NaOH-P_i) under TSP, which indicates greater geochemical capture and thus lower plant availability of P added in the soluble form of TSP compared to less soluble inputs such as PR (e.g., Loganathan et al. 1982; Nziguheba et al. 1998; Rivaie et al. 2008; Zoysa et al. 2001). Increases in Fe- and Al-associated P under soluble additions of P such as TSP have been proposed to result from the lack of synchrony between its rapid solubilization following application and crop P uptake (Savini et al. 2006, 2016; Zoysa et al. 2001). In addition to greater extractable available P (AEM-P_i + NaHCO₃-P_i), the ratio of P_{mic} to labile P indicates that a greater percentage of P applied in the form of Minjingu PR is potentially plantavailable as P_{mic} (Oberson et al. 2006, 2011). Effects of Minjingu PR on soil microbial biomass may reflect a combination of low solubility P additions and liming effects because previous studies indicate that increasing pH alone does not necessarily lead to greater P_{mic} unless combined with low solubility P such as PR (He et al. 1997).

Stimulation of phosphatase activity under P fertilization

This study demonstrates that P fertilization with PR can stimulate phosphatase activity relative to more soluble fertilizer forms such as TSP. Greater acid phosphomonoesterase activity under Minjingu PR relative to TSP could be explained by elevated P-solubilizing bacteria populations observed after only 3 cropping systems at our site (Ndungu-Magiroi et al.



2015) because P-solubilizing bacteria secrete phosphatases as part of their P acquisition portfolio (Jones and Oburger 2011). On the other hand, alkaline phosphomonoesterase activity did not respond to P fertilizer form, though it is considered to be solely of microbial origin (Nannipieri et al. 2011; Spohn and Kuzyakov 2013a) and in weathered soils can be more sensitive than acid phosphomonoesterase to management (Cui et al. 2015). Greater activity of acid phosphomonoesterase, but not alkaline phosphomonoesterase and phosphodiesterase, under Minjingu PR relative to TSP, and under P fertilization relative to no P-fertilization, may be mediated by changes in pH. Fertilization with Minjingu PR shifted soil pH toward the optimum for acid phosphomonoesterase activity (pH 5.2; Hui et al. 2013), but still considerably below the pH considered optimal for alkaline phosphomonoesterase (pH 11) or phosphodiesterase (pH 8) (Tabatabai 2003). In order to improve understanding of P fertilizer impacts on soil phosphatase activities, future work should consider the relationship between soil phosphatase activities and genes encoding phosphatases because this approach can identify phosphatase origins (e.g., microbial vs fungal) (Acuña et al. 2016; Lagos et al. 2016; Ragot et al. 2017) and how microbial community response to management may translate to changes in phosphatase activity (Cui et al. 2015).

Benefits of P fertilization for microbial and enzymatic P cycling

This study identifies positive impacts of P fertilization on the microbial and enzyme activity components of soil P cycling in a weathered soil. Increased P_{mic} following 13 cropping seasons of P inputs relative to a P-unfertilized control supports previous findings of P_{mic} increases following P addition to weathered soils with low available P (e.g., Gichangi et al. 2010; Mukuralinda et al. 2011). In the P-unfertilized control, the high ratio of P_{mic} to labile P demonstrates the greater relative magnitude of P_{mic} as a plant-available P pool in Pdeficient soils (Oberson et al. 2006, 2011). However, a greater percentage of total P as Pmic under Minjingu PR relative to TSP and P-unfertilized treatments suggests greater accessibility of P from Minjingu PR to soil microbes. This may reflect the potential of poorly soluble inputs such as Minjingu PR to stimulate P-efficient microbial communities (see "Stimulation of phosphatase activity under P fertilization") and greater fixation of P added as TSP (i.e., Fe- and Al-associated P).

Our study additionally demonstrates that P fertilization does not necessarily suppress phosphatase activities in weathered soils. Activity of acid phosphomonoesterase is generally thought to increase in response to P deficiency (Nannipieri et al. 2011; Vance 2008; Vance et al. 2003), but acid phosphomonoesterase and phosphodiesterase activities in P-fertilized soils were higher than in the P-unfertilized (and P-deficient) soils at our site, and higher than in P-deficient weathered soils

in a separate study also in western Kenya (Verchot and Borelli 2005). P fertilization is considered to decrease phosphatase activity because P_i can inhibit microbial expression of these enzymes (Nannipieri et al. 2011). For example, inverse associations between phosphatase activity and soil P_i have been observed in weathered soils in tropical forests (Olander and Vitousek 2000). In contrast, at our site, P_i fractions were not negatively correlated with phosphatase activities, consistent with a lack of acid phosphomonoesterase suppression in Oxisols following high P additions (250 kg P ha⁻¹) in this region (Radersma and Grierson 2004). Similarly, acid phosphomonoesterase suppression did not occur in Oxisols in Brazil following 6 years of cumulative P application of up to 549 kg P ha⁻¹ (Conte et al. 2002) and 797 kg P ha⁻¹ (Costa et al. 2013). In some cases, P fertilization at rates comparable or greater than in this study elevated acid phosphomonoesterase activities, which was attributed to increased SOC (Alvear et al. 2005), organic P (Redel et al. 2007), and microbial biomass (Costa et al. 2013).

Stimulation of phosphatase activities in weathered soils by P fertilization could reflect indirect effects of lifting P constraints to crop productivity. Relieving nutrient limitation favors increased crop biomass production and as a result greater residue additions to soil (Geisseler and Scow 2014; Körschens et al. 2013; Ladha et al. 2011). This is consistent with greater labile and total soil C, and acid phosphomonoesterase activity under P fertilization relative to no P-fertilization at our site. Soil C increases from increased biomass production may stimulate phosphatase activities because mineralization of P_o can be driven by microbial demand for C (Heuck et al. 2015; Spohn and Kuzyakov 2013b), and C has been found to be more limiting than P in P-fertilized weathered soils in western Kenya (Bünemann et al. 2004a, b). P fertilization may have also increased acid phosphomonoesterase activity via enhanced root biomass, because plant roots can be a major source of this phosphatase (Nannipieri et al. 2011; Renella et al. 2006). For example, increases in acid phosphomonoesterase in grassland soils receiving N and P (10 g N, P m⁻² year⁻¹) compared to unfertilized grassland soils were partly attributed to the nearly doubling of root biomass as a result of fertilization (Tian et al. 2016).

Greater permanganate-oxidizable C and a trend toward greater SOC indicate under P fertilization demonstrates that alleviating P deficiency can positively impact SOM cycling. This is in agreement with evidence that SOM accrual in weathered soils is strongly limited by nutrient scarcity (Kirkby et al. 2013). Increases in permanganate-oxidizable C and a trend toward greater SOC with P fertilization are consistent with evidence that permanganate-oxidizable C can be an early indicator of SOM accrual (Lucas and Weil 2012; Weil et al. 2003) and is associated with management practices that promote SOM stabilization (Hurisso et al. 2016).



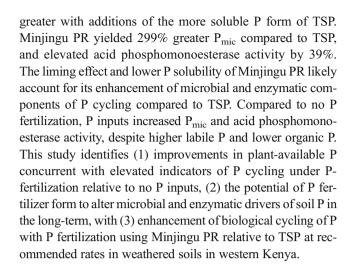
Liming effects of P fertilizers

Phosphate rock additions can have a moderate liming effect (CaCO₃ equivalency >50%) (Sikora 2002) due to proton consumption by PR dissolution, base cation addition (Ca²⁺, Mg²⁺), and CO₃⁻ addition in sedimentary PRs such as Minjingu PR (Chien 1977). At 68% CaCO₃ equivalency, Minjingu PR can be considered a low-grade liming agent (Nekesa et al. 2005), which explains observed pH increases under Minjingu PR additions in this and other studies across East Africa (Szilas et al. 2007b). Assuming a CCE of 68% and given the 12.8% P content of Minjingu PR applied at 50 kg P ha⁻¹ season⁻¹, an equivalent of 3.5 t lime ha⁻¹ had been applied at the time of sampling. Such repeated low-dose liming (0.27 t ha⁻¹ season⁻¹) via Minjingu PR explains its elevation of soil pH (pH 5.35) relative to no P fertilization (pH 4.69) and TSP (pH 5.02). Lesser increases in pH under TSP are attributable to its negligible CaCO₃ equivalency and lower Ca content (12–14%) compared to Minjingu PR (27%) (Havlin et al. 2013; Savini et al. 2016; Szilas et al. 2007b). Liming of weathered soils in western Kenya can improve the availability of native and added P by reducing exchangeable Al3+ and elevating soil pH (Kisinyo et al. 2014, 2015). Thus, Minjingu PR offers benefits beyond recapitalization of soil P for weathered soils in western Kenya.

In addition to indirect effects on soil P cycling by liming, additions of P in the form of Minjingu PR likely contributed greater amounts of nutrients than TSP. The addition of these nutrients, including Ca, Mg, K, Cu, and Zn (Szilas et al. 2007a; Van Kauwenbergh 1991), may explain greater P_{mic} under Minjingu PR relative to TSP. Across field studies in East Africa, an over-yield effect of Minjingu PR relative to TSP at equivalent P rates is generally observed by year 3 (104%) and has been attributable in part to its greater nutrient cation content (Szilas et al. 2007a). In addition to promoting reductions in exchangeable acidity, Ca additions via PR represent a significant input to weathered soils (Khasawneh and Doll 1979), which are generally Ca deficient (Njoku et al. 1987; Sale and Mokwunye 1993; Vitousek et al. 2010). Given that Ca may be an overlooked nutrient limitation in western Kenya (Kihara and Njoroge 2013), Minjingu PR offers additional non-P benefits to farmers in this region.

Conclusion

P fertilization of an acid, weathered soil in western Kenya for 13 cropping seasons produced changes in indicators of biological P cycling depending on the form of fertilizer, Minjingu phosphate rock (PR) or triple super phosphatase (TSP). At equal, recommended application rates (50 kg P ha⁻¹ season⁻¹), labile P was greater under Minjingu PR additions, whereas the less available Fe- and Al-associated pool was



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