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Perennial cover crop biomass contributes to regulating soil P availability more than rhizosphere P-mobilizing capacity in rubber-based agroforestry systems

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ABSTRACT

Cover crops used in agroforestry systems (AFS) are generally perceived to improve soil quality, but mechanisms underlying phosphorus (P) cycling in complex rhizosphere system are less clear, because the impacts of incorporated crops are often determined by inclusion time, residue management and species. We quantified 7-year cumulative effects of perennial legume cover crop–*Flemingia macrophylla* on rhizosphere P cycling and availability during the dry and wet seasons in young and mature rubber-based AFS (i.e., YAFS and MAFS) in tropical China by analyzing cover crop biomass and P content, as well as net rhizosphere changes in P-mobilizing capacity (pH, organic acids and phosphatase activity) and P fractions. Compared to their monoculture counterparts, YAFS enhanced plant biomass and P stock in both seasons, whereas MAFS exhibited an opposite trend, except for increased biomass and P stock of floor litter in the dry season. Moreover, YAFS had a greater effect on net rhizosphere properties by reducing pH and increasing organic acids concentrations and acid phosphatase activity, but MAFS hardly alter them. However, these changes had little effect on net rhizosphere P fractions in both seasons, except the contribution of calcium–P to increasing P availability to a certain extent. Net rhizosphere organic P and microbial biomass P in YAFS were enhanced in both seasons by abundant residue returns from cover crop. Net rhizosphere available P surplus occurred in YAFS in the dry season and maintained balance in the wet season, but it almost reached a deficit in MAFS in both seasons. These results suggest that rhizosphere P cycling was more improved by cover crop in YAFS than MAFS, and biomass of cover crop residue contributed to regulating rhizosphere P cycling and availability more than rhizosphere P-mobilizing capacity. Our study highlights the importance of residue management of permanent cover crops on rhizosphere P cycling and availability in AFS with different ages.

1. Introduction

Phosphorus (P) is an essential limiting nutrient for crop growth and productivity in most agroforestry systems (AFS) (Hinsinger et al., 2011), especially in the tropics, due to the inherently strong binding of P to aluminum (Al) and iron (Fe) (hydr)oxides or low labile organic compounds rather than a small total P (TP) stock (Sugihara et al., 2016; Rodrigues et al., 2021). To overcome P deficiency in soils, phosphate fertilizers are frequently and intensively applied (*ca.* 17.5 Mt P year^{-1}) to sustain crop yields (Plaxton, 2004). However, only a small proportion (10%–20%) of the external P inputs is utilized by crops. Consequently, residual P accumulates in soils over time, resulting in slow P cycling, or is lost to surrounding aquatic ecosystems, often causing eutrophication (Maltais-Landry and Frossard, 2015; Maltais-Landry et al., 2015). This residual P could be sufficient to sustain crop yields worldwide for about 100 years without yield decline if it can be made available (Zhu et al.,

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2018). Moreover, P is derived from a finite and depleted resource, rock phosphate, which renders P fertilizers expensive for some farmers (Sugihara et al., 2016). Therefore, the development of land management practices to better exploit legacy P pools within soils and enhancement of P-use efficiency to reduce reliance on expensive P fertilizers are essential for improving ecologically sustainability of AFS (Richardson et al., 2011).

AFS involve the cultivation of two or more plant species in the same field simultaneously and are considered a promising option for P recycling (Betencourt et al., 2012). In particular, the introduction of cover crops into AFS may stimulate P cycling and improve P availability through biomass retention and rhizosphere effect without reducing the harvest yields of the main crops in addition to providing other ecosystem benefits, such as erosion control, weed suppression and organic matter build-up (Karasawa and Takahashi, 2015; Rodrigues et al., 2021). Cover crops and associated microorganisms can modify rhizosphere processes by altering pH, exuding low-molecular-weight organic acids or stimulating phosphatase activity, either alone or in combination, to mobilize Al/Fe/calcium (Ca)–P and mineralize organic P (P_o), particularly in P-deficient soils (Maltais-Landry et al., 2014; Erel et al., 2017; Sun et al., 2020). Furthermore, apart from biomass quantity of cover crop, its quality (i.e., chemical composition) controls P release and enrichment via mineralization and immobilization of crop residue, (Alamgir et al., 2012). Although the chemical composition of cover crop changes with developmental stage and soil P availability, the magnitude and timing of P mineralization of its residue can be estimated using a general critical value. Cover crop residues with TP content ($>$2.4 g kg^{-1}), carbon (C):P ($<$200) and nitrogen (N):P ($>$10) ratios as well as low lignin ($<$15%) and soluble polyphenol ($<$4%) contents will facilitate net P mineralization (Mukuralinda et al., 2009; Maltais-Landry et al., 2016). P availability is also expected to vary in soils under different residue managements (e.g., surface-placed vs. incorporated and retention vs. removal) (Maltais-Landry, 2015; Wulanningtyas et al., 2021) as even a single cover crop has diverse plant architecture in differently aged plantation systems, thereby influencing residue decomposition and rhizosphere response (Wu et al., 2019). Meanwhile, residue decomposition and rhizosphere processes are affected by climatic and soil conditions during a year, producing seasonal soil P availability (Noack et al., 2014). Although recent studies have investigated the effect of cover crop on P availability, the results are inconsistent because they were conducted in field trials over single seasons. Thus, it remains to be elucidated how continuous crop cover affects P dynamics in no-tillage system during the wet and dry seasons (Hallama et al., 2019).

Rubber tree (*Hevea brasiliensis*) is usually planted as monoculture, replacing natural vegetation and traditional agricultural land in the tropics. Rubber cultivation has covered more than 11.5 Mha globally (Vrignon-Brenas et al., 2019), out of which 1.16 Mha is in tropical China (Li et al., 2019), and its expansion rate is predicted to quadruple by 2050 due to the increasing global demand for natural latex. However, rubber monocultures always initially result in a loss of soil TP and eventually lead to a severe reduction in P availability induced by the accumulation of Al/Fe compounds with increasing soil acidification as stands age (Liu et al., 2018, 2019b). Therefore, fertilizer for rubber plantations is commonly overused, although its application does not resolve the long-term P-deficient condition in rubber monoculture system.

Rubber-based AFS are perceived as contributing to ensure fast returns on investments and ameliorate the negative environmental effects. Thus, rubber plantations are generally intercropped with commercial crops during the immature phase (i.e., no latex is produced for the first ~ 7 years), which has a positive and carry-over effect on rubber growth and latex yield (Vrignon-Brenas et al., 2019). As rubber plantations reach maturity (i.e., ready for rubber tapping), canopy closure and well-developed root systems of rubber trees restrict the yields of intercrops, resulting in a negative benefit under fine management (Li et al., 2019). Interplanting cover crops between rubber plantations, especially perennial legumes used as surface-placed residue rather than for harvest, is an environmentally feasible practice over the entire rubber life cycle (Clermont-Dauphin et al., 2016; Liu et al., 2019a). Our previous study revealed that young rubber plantation intercropped with legume cover crop increased P availability and utilized legacy P_o in bulk soils (0–60 cm) during a year, whereas P species remained constant while intercropping with mature rubber (Liu et al., 2018). However, the knowledge of how rubber-based AFS with different ages affect P availability underlying complex rhizosphere mechanisms is unavailable.

This study aimed to evaluate the short-term (7 years) impact of perennial legume cover crop on rhizosphere P dynamic and availability during the dry and wet seasons in two rubber-based AFS of different ages located on P-deficient soil in southwest China. This was achieved by determining the biomass and nutrient content of litter and fine root, rhizosphere properties and soil P fractions. We hypothesized that: i) legume cover crop would increase residues biomass and P stock in rubber-based AFS, resulting in high mineralization potential; ii) legume cover crop would stimulate rhizosphere P mobilization by modifying rhizosphere properties in rubber-based AFS, resulting in high soil P availability; iii) P mobilization rate would enhance when entering the wet season, irrespective of the rubber stand age.

2. Materials and methods

2.1. Site description

This study was carried out in the environment-friendly rubber plantations (21°33′N, 101°28′E; 880 m above sea level) of Xishuangbanna Tropical Botany Garden, Chinese Academy of Sciences, in Yunnan Province of southwestern China. The climate of the region is characterized by tropical monsoon, with a dry season between November to April and a wet season between May to October. During the experimental period of 2017, the rainfall was 1485.4 mm, with 81.4% occurring in wet season. The mean annual temperature was 22.7 °C, with a monthly maximum of 26.5 °C in June and a minimum of 17.1 °C in December (Fig. S1). The soil type is classified as Oxisol according to USDA Soil Taxonomy, with 32% sand, 32% silt and 36% clay on average.

2.2. Experimental design

The site was mainly covered by rubber monoculture plantation, established in 1994 and 2006, and arranged in a conventional spacing of 2.5 m × 8 m. In June 2010, the perennial leguminous species–*Flemingia macrophylla* were intercropped as cover crop (0.8 m × 1.0 m, 7 lines) in the inter-row spacing between the rubber trees in a section of monoculture stands (i.e., young and mature rubber-based AFS; YAFS and MAFS). Corresponding young and mature rubber monoculture (YM and MM) without the intercrop of *F. macrophylla* were randomly selected as the control. *F. macrophylla*, a fast-growing N_2-fixing shrub, is well adapted to infertile soil with low pH ($<$4.5) and Al toxicity and can produce a large amount of biomass residue for green manure. All stands were managed under local agricultural practice, which involve application of about 0.5 kg of multiplex fertilizer to a 20-cm deep trench during the dry and wet seasons each year. The legume crops were pruned to approximately 30 cm above the ground at the end of each year, and their residues subsequently covered on the soil surface in situ. Each stand type had three independent replicate plots (500 m^2). A detailed description of the stand characteristics is available in Liu et al. (2018) and Liu et al. (2019b).

2.3. Soil sampling scheme

Soil samples were collected in dry season (March) and wet season (August) of 2017. Rhizosphere in this study was operationally defined as the soil volume extending to approximately 2 mm from the living fine root ($<$2 mm diameter) surface, which is equivalent to the usual size of P depletion zones (Hinsinger et al., 2011). In each plot of the AFS, nine evenly distributed soil pits (20 cm × 20 cm × 20 cm) were dug at mid-distance of inter-row area between the rubber trees, placed in the center of the plot to avoid edge impact. After collecting respective living fine roots of rubber tree (inter-rubber) and *F. macrophylla* (inter-*Flemingia*) from the combined soil pits, the rhizosphere soils adhering to fine roots were gently brushed off with a paintbrush for each species. To differentiate the two species, we used size, color and smell of the fine roots as described below 1) rubber tree: fragile, brown and white latex; 2) *F. macrophylla*: flexible, yellow or light brown, special odors and root nodule. This can avoid confusion from common approach of combining the rhizosphere of the two intercropped species for analyses (Tang et al., 2014). The same sampling method is used in the rubber monoculture (mono-rubber) as the AFS plots. For each plot, the rhizosphere soils from all pits were bulked as a single sample. The soils that had no contact with roots were collected as bulk soils. Meanwhile, the floor litter (20 cm × 20 cm) and living fine roots were collected, oven-dried at 70 °C to a constant weight. P stock of plant samples was calculated by multiplying P content and their biomass per unit area.

2.4. Soil chemical characterization

Soil pH was measured in a 1:2.5 soil-water mixture with a pH meter (FE28-Standard, Mettler Toledo, Germany). The contents of total C and N were analyzed by dry combustion with an elemental analyzer (VarioMAX CN, Elementar Analysensysteme GmbH, Germany). The fractionation of inorganic P (P_i) content in soils was measured using a modified Chang and Jackson sequential procedure (Yang et al., 2010). Briefly, 1.0 g soil sample was extracted with 0.5 M NH_4F (Al–P), 0.1 M NaOH (Fe–P), and 0.25 M H_2SO_4 (Ca–P). At each step, samples were shaken with 30 mL of solution (1 h, 200 rpm end-over-end), followed by centrifugation at 4500 rpm for 10 min and filtration through a 0.45 μm membrane, and P analyses on the supernatant by inductively coupled plasma atomic emission spectrometry (ICP-AES, Thermo Fisher iCAP6300, USA). P_o content was determined by an ignition method (Yang et al., 2010). TP content was digested using $HClO_4$–HF and determined by ICP-AES. Available P (AP) content was extracted with 0.03 M NH_4F–0.025 M HCl and analyzed using a segmented flow analyzer (Auto Analyzer 3, SEAL Analytical GmbH, Germany). Microbial biomass P (P_{mic}) content was extracted with 0.5 M $NaHCO_3$ and estimated as the difference between the fumigated and unfumigated soil divided by a correction factor of 0.4 (Liu et al., 2019a). Additional physicochemical properties of the soil are presented in Tables S1 and S2.

The activity of acid phosphatase (APA) was determined using *p*-nitrophenyl phosphate (pNPP) as substrate method (Tabatabai and Bremner, 1969). Briefly, 5 g of soil was incubated in 20 mL of 0.5% pNPP solution prepared with acetate buffer (pH 5.0) at 37 °C for 24 h. The release of phenol was determined colorimetrically at 660 nm, using 2,6-dibromchinone-chlorimide as coloring reagent. Controls had substrate solution replaced by water, and calibration blanks contained no soil.

Total organic acid (TOA) concentration was extracted by shaking 2 g of soil with 10 mL of 0.1% H_3PO_4 for 1 min according to Maltais-Landry et al. (2014). The extracts were centrifuged at 5000 rpm for 5 min and filtered through a 0.45 μm membrane to collect aqueous phase. The aqueous samples were determined by HPLC with a Waters 2695 Alliance separations module and 996 photodiode array detector (Waters, Milford, MA) using 0.1% H_3PO_4/acetonitrile (98:2, v/v) as mobile phase (pH 2.2). A reverse-phase column of Capcell Pak C18 (5 μm, 250 × 4.6 mm, Shiseido, Tokyo) was used at a flow rate of 1 mL min^{-1} controlling the column temperature at 35 °C. A total of 20 μL of the extract and mixed standards (Sigma-Aldrich, St-Louis, MO) were injected into HPLC, and quantified at 210 nm.

2.5. Statistical analyses

All dependent variables of the same-aged rubber stand were analyzed using two-way analysis of variances (ANOVA) with season and management as fixed factors, followed by a Duncan's multiple range test at $P < 0.05$ level. A delta change (Δ) in soil parameters between rhizosphere and bulk soils (Table S3) was calculated to interpret net rhizosphere effect by avoiding variation among plots as described by Maltais-Landry et al. (2014). A positive or negative rhizosphere change indicates a relative high pool in the rhizosphere or bulk soil, respectively (Fu et al., 2020). We considered that difference between rhizosphere soil of a given species and bulk soil was significant if the 95% confidence interval deviated from zero (Almeida et al., 2018). Meanwhile, a simple *t*-test was used to determine significant difference between mono- and intercropping (averaging delta values of two inter-species) within a given season. Pearson correlation analysis was applied between P fractions and plant, physical-chemical characteristics of soils. All statistical analyses were performed using Version 9.1 (SAS Institute Inc., Cary, USA).

3. Results

3.1. Biomass and P stock of floor litter and fine root

Floor litter biomass and P stock of young system were significantly affected by season, management and their interactions ($P < 0.05$), except for seasonal effect on litter biomass ($P = 0.83$, Table 1). Their levels were higher in YAFS than YM in the dry season, while remained relatively constant in the wet season (Fig. 1a and c). A significant interaction between season and management on floor litter biomass and P stock occurred in mature system ($P < 0.05$, Table 1). In MAFS, floor litter biomass decreased in the wet season and P stock increased in the dry season compared to MM (Fig. 1b and d).

Fine root biomass and P stock of young system were significantly affected by season, while P stock of mature system was dramatically influenced by season and management ($P < 0.05$, Table 1). Their levels in YAFS were slightly high relative to YM in both seasons, but presented an opposite trend for mature system, especially with an obvious decrease in P stock in the dry season (Fig. 1).

3.2. Soil pH, organic acid concentration and acid phosphatase activity

In both systems, pH value of rhizosphere soils was generally lower than bulk soils (Fig. 2a and b), and significantly varied with season, management and their interactions ($P < 0.05$), except for the effect of management in young system ($P = 0.98$, Table 1). Net rhizosphere soil pH was lower in YAFS than YM in the dry season, whereas a contrary pattern was observed in the wet season, especially in soil associated with inter-*Flemingia* (Fig. 2a). MAFS did not alter net rhizosphere soil pH in the dry season, but significantly decreased its value in the wet season relative to MM, which was mainly observed in the lowest rhizosphere pH of inter-rubber (Fig. 2b). Moreover, rhizosphere soil pH of inter-*Flemingia* was always larger than inter-rubber regardless of stand age and season, except for a 0.3-unit reduction in the dry season for young system.

TOA concentration in both systems was consistently greater in rhizosphere soils compared to bulk soils (Fig. 2c and d), and was significantly affected by season, management and their interactions ($P < 0.05$), except for management effect in young system ($P = 0.13$, Table 1). YAFS rhizosphere soils had higher net TOA concentration than YM in the dry season, but no difference was observed in the wet season (Fig. 2c). MAFS did not alter net TOA concentration in the dry season, but significantly increased it in the wet season relative to MM, which was primarily observed in the highest value of inter-rubber (Fig. 2d). TOA concentration of young system was significantly and positively associated with acetate ($r = 0.52$, $P < 0.05$) and citrate ($r = 0.74$, $P < 0.01$) in the dry season, while with malate ($r = 0.51$, $P = 0.051$) and tartrate ($r = 0.55$, $P < 0.05$) in the wet season for mature system (Fig. S2). Accordingly, the net variation of TOA contributed to the reduction of rhizosphere soil pH (young-dry and mature-wet: $r > -0.83$,

Table 1

Results (*F*-value) of two-way ANOVA testing the effects of season (S), management (M) and their interactions on plant and soil parameters in two-aged rubber agroforestry systems. Significance level: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Abbreviations: TOA, total organic acid; APA, acid phosphatase activity; Al/Fe/Ca–P, aluminum/iron/calcium–P; P_o, organic P; P_{mic}, microbial biomass P; AP, available P; TP, total P.

Factors	Floor litter		Fine root		Soil (rhizosphere–bulk)								
	Biomass	P stock	Biomass	P stock	Δ pH	Δ TOA	Δ APA	Δ Al/Fe–P	Δ Ca–P	Δ P_o	Δ P_{mic}	Δ AP	Δ TP
Young system													
S	< 0.1	42.1^{***}	6.3*	20.0^{**}	5.2*	5.0*	1.7	3.8	22.2^{***}	5.6*	2.4	6.9*	4.3
M	13.1^{**}	63.4^{***}	5.2	1.7	< 0.1	2.4	20.7^{***}	0.2	5.7*	13.1^{***}	17.8^{***}	18.5^{***}	9.8^{**}
S × M	7.5*	30.9^{**}	< 0.1	2.2	19.4^{***}	7.4^{**}	1.2	0.6	13.5^{**}	0.3	0.8	2.8	3.2
Mature system													
S	0.5	0.2	5.2	11.4^{**}	41.0^{***}	21.3^{***}	61.6^{***}	27.3^{***}	21.7^{***}	11.1^{**}	27.1^{***}	31.0^{***}	0.6
M	0.9	0.2	3.0	10.5*	25.0^{***}	13.2^{**}	3.2	8.4^{**}	10.4^{**}	1.5	1.3	47.6^{***}	4.5*
S × M	9.6*	9.2*	< 0.1	1.0	14.5^{**}	13.0^{**}	1.5	6.3*	3.6	4.9*	3.2	8.6^{**}	3.7

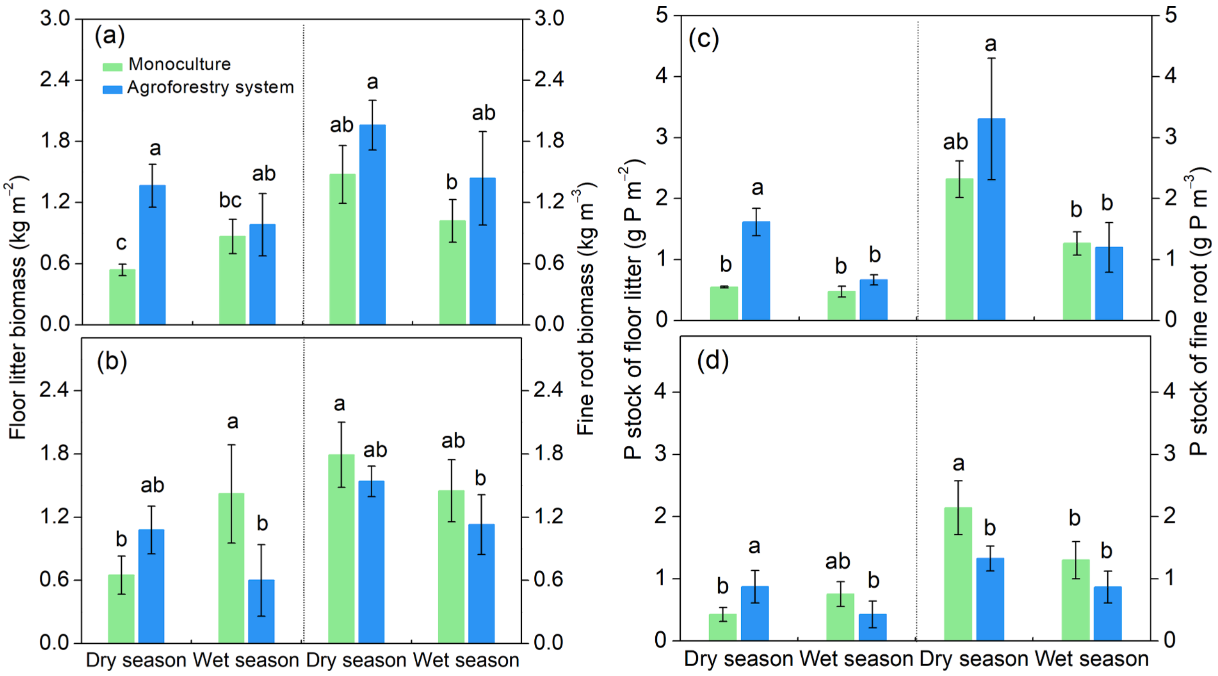

Fig. 1. Biomass and P stock of floor litter (left) and fine root (right) in young (a, c) and mature (b, d) rubber monocultures (YM and MM) and agroforestry systems (YAFS and MAFS) during the dry and wet seasons. Error bars are 95% confidence intervals of the mean. Different letters indicate significant differences computed by a Duncan's test ($P < 0.05$).

$P < 0.01$, Fig. S3).

APA in both systems was consistently higher in rhizosphere soils than bulk soils (Fig. 2e and f), and was strongly influenced by management in young system and by season in mature system, respectively ($P < 0.001$, Table 1). Net APA was greater in YAFS than YM in both seasons (Fig. 2e), whereas in mature system, management had no impact in both seasons, despite being with distinct variation among mono- and inter-species in the wet season (Fig. 2f).

3.3. *Soil P fractions and availability*

In both systems, Al/Fe–P was basically enriched in rhizosphere soils than bulk soils (Fig. 3a and b), and was significantly affected by season, management and their interactions only in mature system ($P < 0.05$, Table 1). There was no difference in net Al/Fe–P between AFS and monoculture in both seasons, except for a decline in MAFS relative to MM in the dry season, which was mainly observed in the lowest content of inter-*Flemingia*.

Rhizosphere soils were generally depleted in Ca–P compared to bulk soils in both systems (Fig. 3c and d), and Ca–P significantly varied with season, management and their interactions ($P < 0.06$, Table 1). Compared to YM, YAFS resulted in higher net Ca–P depletion in the dry season, but more its accumulation in the wet season, especially in soil associated with inter-*Flemingia* (Fig. 3c). In contrast, MAFS depleted more net Ca–P in the wet season compared to MM (Fig. 3d).

P_o enrichment was greater in rhizosphere soils than bulk soils in both systems (Fig. 3e and f), and was strongly influenced by season and management ($P < 0.05$), except for the effect of management in mature system ($P = 0.27$, Table 1). YAFS accumulated more net P_o than YM in both seasons, but MAFS did not alter net P_o content relative to MM.

More P_{mic} was immobilized in rhizosphere soils than bulk soils (Fig. 3g and h), and was significantly affected by management in young system and by season in mature system, respectively ($P < 0.001$, Table 1). In both seasons, YAFS led to greater net P_{mic} storage than YM, while MAFS did not affect net P_{mic} content, despite the obvious variation among mono- and inter-species in the wet season.

AP content in both systems was higher in rhizosphere soils than bulk soils (Fig. 4), and was obviously affected by season, management and their interactions ($P < 0.05$), except for the interactive effect in young system ($P = 0.10$, Table 1). YAFS significantly increased net AP content in the dry season relative to YM, mainly due to the highest content of inter-rubber; the rhizosphere effect was not significant in the wet season

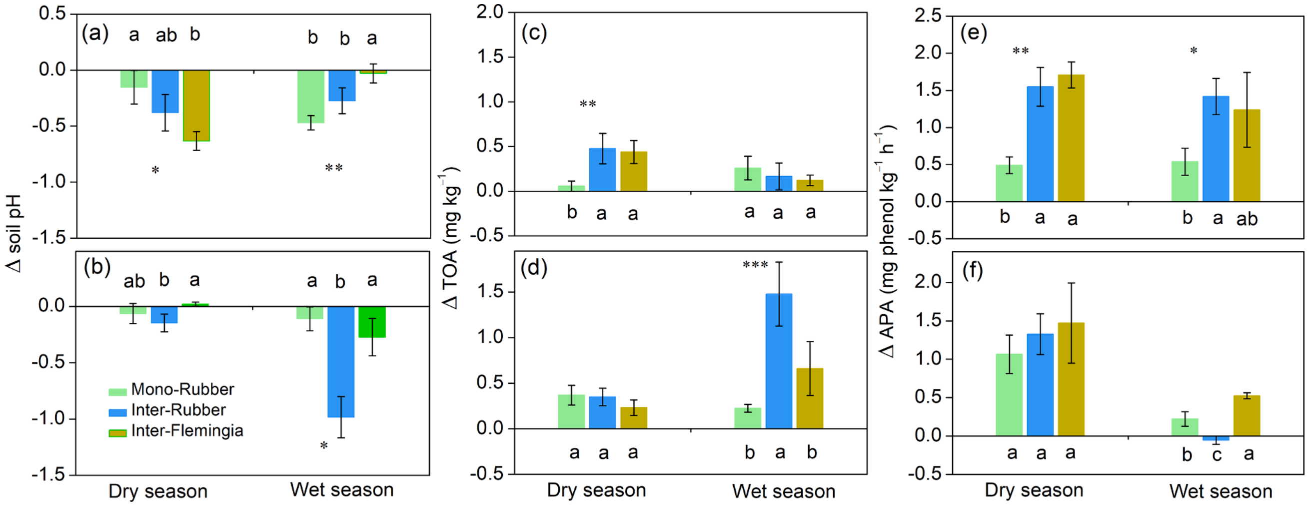

Fig. 2. Delta soil pH, total organic acid (TOA) concentration and acid phosphatase activity (APA) (rhizosphere–bulk) in young (a, c, e) and mature (b, d, f) rubber monocultures (YM and MM) and agroforestry systems (YAFS and MAFS) during the dry and wet seasons. Error bars are 95% confidence intervals of the mean. Different letters indicate significant differences among rhizospheres (i.e., mono-rubber, inter-rubber and inter-*Flemingia*) within each season computed by a Duncan's test ($P < 0.05$). Asterisk within a given season shows statistical difference between monoculture and intercropping (averaging delta values of two inter-species). Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

(Fig. 4a). MAFS dramatically decreased net AP content in both seasons compared to MM (Fig. 4b).

3.4. Relationship between P fractions and other attributes

The correlations among relative changes (rhizosphere–bulk) in soil P fractions and plant or soil attributes were inconsistent for the two systems during the dry and wet seasons (Tables S4 and S5). For example, the changes in P_o or P_{mic} was significantly positively correlated with floor litter biomass ($r > 0.71$, $P < 0.05$) and P stock ($r > 0.84$, $P < 0.01$) of young system in the dry season, whereas Ca–P showed a negative correlation with them ($r > -0.72$, $P < 0.05$). Moreover, the net effect of these changes in P fractions on AP and TP was not straightforward, with variable results for both seasons (Table S5). However, we observed a strong, positive linear relationship between net rhizosphere change in AP and TP (young system: $r > 0.86$, $P < 0.01$; mature system: $r > 0.71$, $P < 0.05$ for both seasons, Fig. 5).

4. Discussion

4.1. P cycling via plant biomass

The cover crop biomass, P content and chemical composition affect P release during its residue decomposition in AFS, particularly P_i that is the major pool in the plant tissue (~50%) (Damon et al., 2014), which fluctuates with season and stand age (Soltangheisi et al., 2018). Seven-year continuous covering of *F. macrophylla* increased floor litter biomass and P stock of rubber-based AFS in the dry season (Fig. 1). *F. macrophylla* possesses a great capacity to absorb labile P from the subsoil, resulting in a substantial increase in aboveground biomass P stock before pruning (Liu et al., 2018), which is protected from sorption onto the Al/Fe minerals (Alamgir et al., 2012). This is evident by the fact that P release of litter residue is inhibited in rubber-based AFS relative to monocultures in the dry season (Tongkaemkaew et al., 2018). On entering the wet season, residual P was readily released into AFS soils by increased decomposition rate via leaching by rainfall (Erinle et al., 2018) and chemical alteration by soil organisms (Varela et al., 2017). Indeed, approximately 60% of the initial P is released from legume (*Pueraria phaseoloides*) residues within 75 days after mulching in rubber monoculture from the beginning of the wet season (Clermont-Dauphin et al., 2016). These results support our first hypotheses that AFS had a relatively fast mineralization potential and P release, especially YAFS due to abundant litter residues with lower C:P and diverse decomposer communities, as exhibited by double P availability (Liu et al., 2018, 2019a). However, high litter residue P may decrease P_{mic} turnover, increase soil P_o and limit P availability, suggesting how P enrichment may instead lower P cycling rate (Alamgir et al., 2012; Maltais-Landry et al., 2014). Similar to a *meta*-analysis finding (Hallama et al., 2019), our results proved that aboveground residues of cover crop is favorable in controlling soil P cycling in rubber-based AFS.

Fine root decomposition has comparable P release (per unit of biomass) to the litter residues (Damon et al., 2014). YAFS increased fine root biomass and P stock in the dry season (Fig. 1), which is associated with root proliferation for foraging P nutrient and water at the surface layer during leaf-flushing (Clermont-Dauphin et al., 2018). In contrast, MAFS decreased P absorption by niche facilitation of fine root in the dry season, implying a high P-use efficiency of mature rubber with moderate interspecific competition after introducing *F. macrophylla* (Liu et al., 2018). This is supported by mature (25-year-old) rubber monoculture where root growth is more vigorous than rubber-*F. macrophylla* AFS in the dry season, creating drought resistance (Wu et al., 2016). Fine roots grow slowly during the ensuing wet season, in parallel with increased decomposition and vegetative stage (e.g., rubber tapping). This induces more root P allocation to the aboveground parts of plants, especially in YAFS wherein a one-fold decrease in fine root P can be constantly replenished by litter P (i.e., P retranslocation). From rubber immature to peak tapping period, fine root biomass and top-down transport of P declined evidently with high soil moisture (Lin et al., 2011). These changes are in line with reports that fine root growth increases during the dry season compared to the wet season (Lima et al., 2010), and its growth dynamics determine P release in acidic soils linking to litter response (Rose et al., 2010; Contador et al., 2015).

4.2. Net rhizosphere P-mobilizing capacity

Net rhizosphere acidification in YAFS occurred in the dry season (Fig. 2a), which is associated with extensive exudation of organic acids by denser roots and microorganisms (Fig. 2c) and not via symbiotic N_2-fixation because few nodules were observed in *F. macrophylla* roots, although legume typically acidify rhizosphere rely on high rate of N_2-fixation (Hinsinger et al., 2011). This is confirmed by a positive correlation between rhizosphere pH and organic acids, driven by citrate and

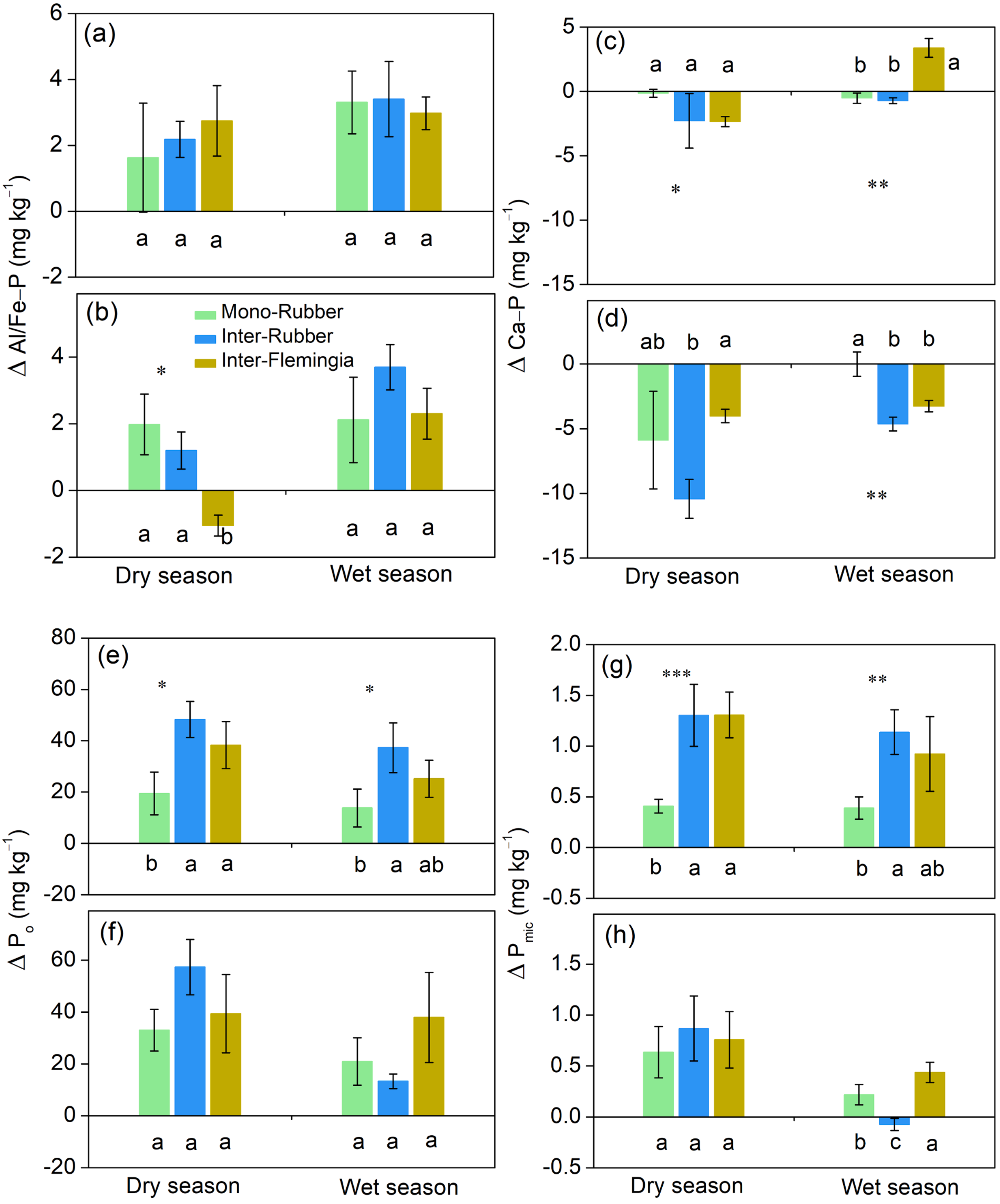

Fig. 3. Delta soil P fractions (rhizosphere–bulk) in young (a, c, e, g) and mature (b, d, f, h) rubber monocultures (YM and MM) and agroforestry systems (YAFS and MAFS) during the dry and wet seasons. Error bars are 95% confidence intervals of the mean. Different letters indicate significant differences among rhizospheres (i.e., mono-rubber, inter-rubber and inter-*Flemingia*) within each season computed by a Duncan's test ($P < 0.05$). Asterisk within a given season shows statistical difference between monoculture and intercropping (averaging delta values of two inter-species). Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

acetate (Figs. S2 and S3). Conversely, net increase in rhizosphere pH in the wet season was mostly associated with inter-*Flemingia* (Fig. 2a), as reported for other legumes in P-deficient acidic soils (Li et al., 2010; Rose et al., 2010). This could be attributed to preferential uptake of NO$_3^-$ and the subsequent release of OH$^-$ into the rhizosphere to maintain charge balance (Sugihara et al., 2016), or ammonification of fine root residue N of inter-*Flemingia* (Li et al., 2010). MAFS root-induced net acidification in the wet season mainly resulted from higher organic acids release of inter-rubber (Fig. 2b and d), especially malate and tartrate, which can dissolve non-labile P (i.e., Ca–P) to meet the need for latex (Fig. 3d). Notably, higher rhizosphere pH of inter-*Flemingia* than inter-rubber in both seasons commonly suggested an important role of *F. macrophylla* in alleviating Al toxicity and acidity-induced P deficiency for rubber growth and yield in AFS (Sugihara et al., 2016).

YAFS increased net rhizosphere APA in both seasons (Fig. 2e), which could occur either directly by secretion of the large fine roots or

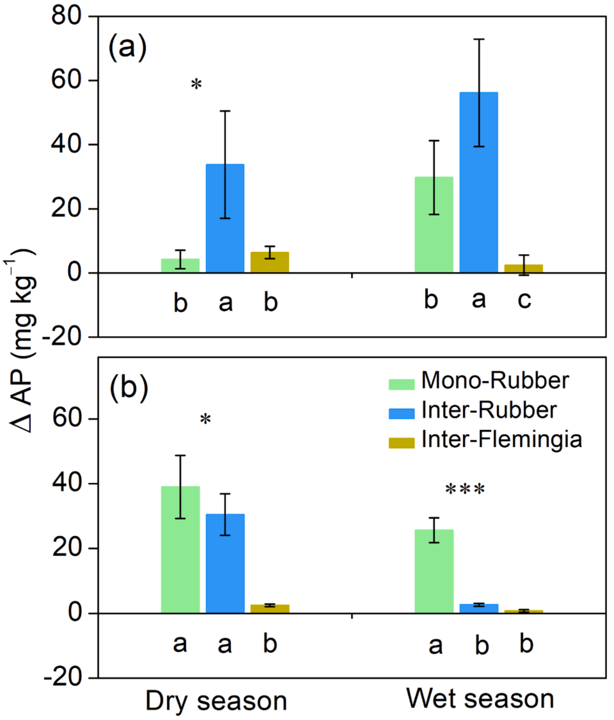

Fig. 4. Delta soil available P (AP) (rhizosphere–bulk) in young (a) and mature (b) rubber monocultures (YM and MM) and agroforestry systems (YAFS and MAFS) during the dry and wet seasons. Error bars are 95% confidence intervals of the mean. Different letters indicate significant differences among rhizospheres (i.e., mono-rubber, inter-rubber and inter-*Flemingia*) within each season computed by a Duncan's test ($P < 0.05$). Asterisk within a given season shows statistical difference between monoculture and intercropping (averaging delta values of two inter-species). Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

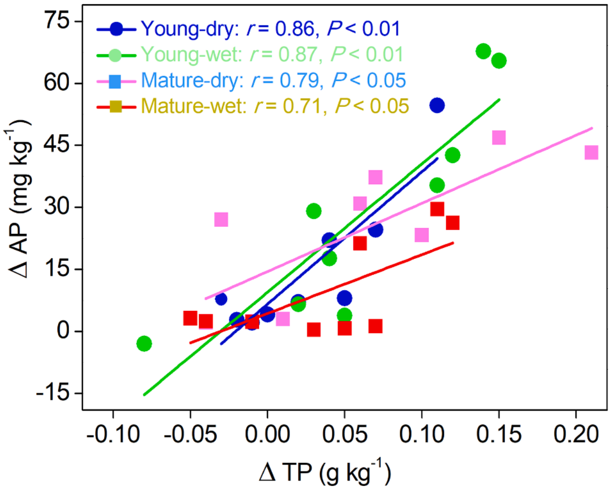

Fig. 5. Relationship between net change in soil available P (AP) and total P (TP) (rhizosphere–bulk) in young (circle) and mature (square) rubber agroforestry systems during the dry and wet seasons.

indirectly by stimulation of rhizosphere microbial activity driven by abundant organic matter (Table S2). Li et al. (2019) also reported that high rhizosphere C substrates will stimulate microorganisms to secrete more phosphatase in rubber-calla lily (*Alocasia macrorrhizos*) intercropping. However, MAFS had no net rhizosphere effect on APA (Fig. 2f), indicating a relatively small soil P_o mobilization. Similarly, APA contribute less to rhizosphere P mobilization than pH and organic acids in maize (*Zea mays*)-alfalfa (*Medicago sativa*) polyculture (Sun et al., 2020). Although N-rich phosphatase positively correlated with plant total N and fine root N:P ($r > 0.60$, $P < 0.05$) in this study, the central role of *F. macrophylla* N_2-fixation in increasing APA could not be validated. This is consistent with a report that phosphatase activity is unrelated to N_2-fixation in tropical forests, regardless of soil P availability (Guilbeault-Mayers et al., 2020), but differs from the finding that phosphatase activity is enhanced by rhizosphere N_2-fixation of legumes (Maltais-Landry et al., 2014). These contradictory results are indicative of legume-specific phosphatase activation. Collectively, partly support our second hypothesis that YAFS had a greater effect on net rhizosphere P-mobilizing capacity, but MAFS hardly alter it.

4.3. Net changes in rhizosphere P fractions

The constant net rhizosphere Al/Fe–P in AFS in both seasons could be explained by the relatively small changes (<threshold of 5 μM g^{-1} soil) in organic acids (Figs. 2 and 3) that cannot desorb Al/Fe–P effectively (Richardson et al., 2011). This weak effect of organic acids on rhizosphere P_i availability has been observed in other P-deficient agricultural soils (Maltais-Landry et al., 2014; Wang et al., 2016). However, net Al/Fe–P reduction in MAFS in the dry season, was mainly due to increased rhizosphere pH of inter-*Flemingia*, reflected by a negative correlation between Al/Fe–P and pH (Table S5). This correspond with decline in P stock of fine roots during this phase (Fig. 1d), and may lead to high Al/Fe-(hydr)oxides tightly absorbing P_i to form non-labile P (Yang et al., 2010; Aleixo et al., 2020). The solubility of net rhizosphere Ca–P was highly pH-dependent and species-independent (Fig. 3c and d), indicating the interspecific species regulation in AFS based on their demand for P.

Net accumulation of rhizosphere P_o was observed in YAFS despite higher APA in both seasons (Fig. 3e), attributing to organic matter return and diversity of rhizodeposits from rich *F. macrophylla* residues, whereas both P_o and APA were constant in mature system (Fig. 3f). These are in contrast to several studies conducted on P-deficient acidic soils, where P_o is the pool most affected by cover crops and depleted by high APA hydrolysis before uptake by plants (Rose et al., 2010; Maltais-Landry and Frossard, 2015; Chen et al., 2016). The differences indicate that P_o mineralization is not necessarily facilitated by high APA alone unless there is a concurrent increase in the solubility of P_o forms, controlling by rhizosphere pH (George et al., 2002). In acidic soils, P_o is more stable and mineralization rate is slower (Damon et al., 2014), so mineralization is fast in young system (rhizosphere pH > 5.5). A decline in P_o pool from the dry to wet season in two systems following by synchronous change in P_{mic} suggested that a portion of labile P_o (i.e., $NaHCO_3$-P_o) is continuously utilized by rubber tapping at relatively short timescales (Liu et al., 2018).

Increased net rhizosphere P_{mic} in YAFS was observed in both seasons (Fig. 3g), consistent with the finding for cereal intercropped with legumes (Tang et al., 2014). This is due to higher rhizosphere microbial biomass immobilizing P_i released from *F. macrophylla* residues, which is temporarily stored and subsequently available to rubber trees (Rose et al., 2016). In contrast, MAFS did not alter P_{mic} (Fig. 3h), similar to the result that there were no differences in rhizosphere P_{mic} among treatments when wheat (*Triticum aestivum*) and legume growing in monoculture or as a mixture (Wang et al., 2011). However, a considerable seasonal variability in P_{mic} was observed in mature system, indicating that rhizosphere P_{mic} as a more active P pool due to fast turnover can be utilized by rubber tapping in the wet season, although it accounts for less than 5% of TP (Boitt et al., 2018), because the majority of P released upon drying-rewetting processes originates from microbial biomass under P deficiency (Zhang et al., 2020).

Net rhizosphere AP increased in YAFS in the dry seasons, mainly observed in inter-rubber (Fig. 4a), suggesting rhizosphere AP is surplus, which is related to continuous Pi release from *F. macrophylla* residue. In the wet season, management effect was eliminated by inter-*Flemingia* due to Ca–P adsorption with higher rhizosphere pH. However, MAFS decreased net rhizosphere AP in both seasons (Fig. 4b), indicating AP is almost deficient, particularly in the wet season. Li et al. (2019) found Calla lily intercropping in rubber plantations depletes less net rhizosphere AP and TP than monocropping with a negative rhizosphere effect. Collectively, few correlations were observed between net rhizosphere AP and plant as well as other soil parameters (Tables S4 and S5), which means complex root-induced processes are involved in the control of rhizosphere P availability in AFS at specific time (Betencourt et al., 2012; Erel et al., 2017). However, the net change in AP was significantly positively correlated with TP in both systems throughout the year (Fig. 5), consistent with the finding of Maltais-Landry et al. (2014) and Li et al. (2019). This indicates the variations in net rhizosphere AP are largely driven by changes in TP rather than individual P fractions. Furthermore, the slope reflected net rhizosphere TP turnover was faster in young than mature system where greater contribution existed in the dry season.

4.4. Implications of cover crops on P cycling in the region

The interaction between cover crops and soil P fate is complex, and region-specific recommendations are needed (Hallama et al., 2019). More than 70% of rubber plantations in China are mature stands, resulting in soil P depletion (Li et al., 2019). Thus, rubber-cover crop AFS are designed to benefit from increased P cycling and availability. Many perennial legumes intercropped as cover crop into rubber plantation have been shown to improve P availability in bulk soils (Table S6), thereby facilitating P uptake by rubber trees (Clermont-Dauphin et al., 2016). This is mainly because of high dry matter accumulation and favorable crop residue stoichiometry, leading to rapid mineralization at the soil surface. Unfortunately, the influence of rhizosphere processes of perennial cover crops on P cycling has not been elucidated. Cover crops with well-developed root systems and rhizospheres (i.e., structure and function) are promising long-term soil P recyclers and solubilizers (Hinsinger et al., 2011; Soltangheisi et al., 2018). Thus, the cutting regime of cover crops should be adjusted for reconstruction of root system, increasing the capacity of main crop to acquire P. We found that surface-placed *F. macrophylla* had contrasting seasonal effects on rhizosphere P cycling and availability in rubber-based AFS, which can reduce P fertilizer inputs due to potential cumulative effect of 7-year continuous covering that returned high-P residues to soil, thereby leading to accumulation of organically-cycled P and shielding of P adsorption sites (Damon et al., 2014). However, more conclusive results on residue P cycling are needed from permanent cover crop management under a changing regional climate.

5. Conclusions

This study found contrasting seasonal effects of perennial cover crop on rhizosphere P cycling after 7-year of surface-placed residues of *F. macrophylla* under no-till acidic soil in rubber-based AFS. Compared to respective monocultures, YAFS increased plant biomass and P stock in both seasons, but MAFS decreased their levels, except for increased biomass and P stock of floor litter in the dry season. Furthermore, YAFS and MAFS respectively decreased net rhizosphere Ca–P in the dry season and wet season by reducing rhizosphere pH. Net rhizosphere P_o and P_{mic} in YAFS were enhanced in both seasons mainly as a result of abundant organic matter return from *F. macrophylla* residues despite with higher APA, but they almost remained stable in MAFS. High net rhizosphere AP mainly induced by inter-rubber of YAFS was observed in dry season, but this management effect was eliminated by inter-*Flemingia* in the wet season. In contrast, MAFS decreased net rhizosphere AP of inter-species in both seasons. Our results suggest that rhizosphere P cycling and availability were more significant in YAFS than MAFS, and biomass of *F. macrophylla* residue is more beneficial than other factors in controlling rhizosphere P cycling processes in rubber-based AFS. Although the inter-rubber approach improves rhizosphere P status to some extent, the lack of direct economic income for smallholders limits the expansion of this model; thus, comprehensive value of inter-*Flemingia* should be investigated. Further research is needed to explore how rhizosphere microorganisms affect P cycling at different soil depths involving roots thickness and how much P fertilizer can be reduced by introducing different cover crops in AFS with different ages.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.115218.

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