Leaf litter inputs decrease phosphate sorption in a strongly weathered tropical soil over two time scales

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Abstract In strongly weathered soils, leaf litter not only returns phosphorus (P) to the soil environment, it may also modify soil properties and soil solution chemistry, with the potential to decrease phosphate sorption and increase plant available P. Using a radioactive phosphate tracer (^{32}P) and 1 h laboratory incubations we investigated the effect of litter inputs on phosphate sorption over two time scales: (1) long-term field litter manipulations (litter addition, control and litter removal) and (2) pulses of litter leachate (i.e. water extracts of leaf litter) from five species. Leachate pulse effects were compared to a simulated throughfall, which served as a control solution. Soil receiving long-term doubling of leaf litter maintained five-fold more phosphate in solution than the litter removal soil. In addition to the quantity of phosphate sorbed, the field litter addition treatment decreased the strength of phosphate sorption, as evaluated through extraction of sorbed ^{32}P using a weakly acidic ammonium fluoride solution (Bray 1). In litter removal soil, leachate pulses significantly reduced phosphate sorption in comparison to the throughfall control for all five species evaluated. However, the ability of leachate pulses to reduce phosphate sorption decreased when soil had received field litter inputs. Across soils the effect of leachate pulses on phosphate sorption increased with net sorption of dissolved organic C, with the exception of leachate from one species that had a higher index of aromatic C concentration. These results demonstrate that litter inputs, as both long-term inputs and short-term leachate pulses, can decrease the quantity and strength of phosphate sorption, which may increase the biological availability of this key nutrient.

Keywords Phosphorus · Tropical forest · Nutrient cycling · Dissolved organic carbon · Soil organic matter

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Introduction

In strongly weathered soils much of the phosphate that is removed from solution by either adsorption or precipitation is not readily available for plant uptake due to strong interactions with abundant iron and

aluminum oxides (Fontes and Weed 1996; Mattingly 1975; Uehara and Gillman 1981). Indeed, phosphate sorption by iron and aluminum oxides is one reason phosphorus (P) is often hypothesized to limit net primary productivity of plant communities on strongly weathered soils (Crews et al. 1995; Walker and Syers 1976). Plant uptake of P requires phosphate in soil solution (Barrow 1978; Syers et al. 2008); therefore, mechanisms that decrease the strength and magnitude of phosphate sorption (which in turn increase the amount of phosphate in, and passing through, soil solution) may act as controls on net primary productivity. Organic matter additions have long been hypothesized to play a role in altering soil phosphate sorption (Bauer 1921; Dalton et al. 1952) and proposed mechanisms can be divided into two categories: (i) organic matter effects on increasing microbial competition for soil solution phosphate, and (ii) organic matter effects on soil physicochemical properties. Here we focus on the role of organic matter inputs on altering phosphate sorption through effects on soil chemistry.

Support for the hypothesis that organic matter additions not only serve as P inputs but also have the potential to decrease soil phosphate sorption through physicochemical effects can be found in investigations in agricultural systems (Dalton et al. 1952; Moshi et al. 1974; Negassa et al. 2008; Nziguheba et al. 2000; Ohno and Crannell 1996) and a pine plantation (Bhatti et al. 1998). The ability of litter inputs to influence phosphate sorption through effects on soil chemistry has been less studied in tropical forests. Several lines of reasoning, however, suggest that physicochemical effects of litter on soil P cycling may be most pronounced in these systems. While lowland tropical soils occur on a wide range of soils, many are supported by strongly weathered soils with high phosphate sorption capacities (Fox and Searle 1978; Vitousek and Sanford 1986). Furthermore, lowland tropical forests tend to have both large litter inputs (Vitousek 1984) and rapid litter turnover (Cusack et al. 2009). Therefore, heavy rains, either seasonally or throughout the year, can create high concentrations of dissolved organic carbon (DOC) and solute movement from litter to the soil (Cleveland et al. 2006), which can alter soil solution chemistry (mechanisms are outlined below). Finally, if productivity on strongly weathered soils requires efficient P cycling (Vitousek 1984), decreases in sorption of soil solution phosphate

through litter inputs could constitute a plant strategy to increase growth, survival and reproduction. This suggests that if there are litter characteristics that decrease the quantity and strength of soil phosphate sorption, and increase plant fitness, these traits may be selected for over time (Binkley and Giardina 1998).

Abiotic mechanisms by which organic matter additions can alter soil phosphate sorption include carbon (C) competition for, and occupation of, phosphate sorption sites, in addition to changes in pH and ionic strength (Guppy et al. 2005; Ohno and Crannell 1996). Below we explore each of these potential mechanisms and we focus on two time scales: (1) the cumulative effect of long-term litter inputs on soil chemical properties and (2) the short-term effect of litter leachate pulses on phosphate sorption, which occurs when both leachate and phosphate are simultaneously in solution.

Organic C inputs may reduce phosphate sorption by decreasing available sorption sites (de Mesquita and Torrent 1993; Easterwood and Sartain 1990; Ohno and Crannell 1996; Perrott 1978), although this depends on the chemical nature of the C compounds involved. For example, the presence of some low molecular weight organic compounds, such as oxalate and malate, can greatly decrease phosphate sorption (Bhatti et al. 1998; Kafkafi et al. 1988; Lopez-Hernandez et al. 1986; Nagarajah et al. 1970; Swenson et al. 1949) while other compounds such as simple carbohydrates have no effect (Negassa et al. 2008). The effect of higher molecular weight C compounds is less clear. While humic and fulvic acids may sometimes decrease phosphate sorption to pure iron and aluminum oxides (Hunt et al. 2007, but see Borggaard et al. 2005) and soils (Sibanda and Young 1989), in other instances high molecular weight organic C compounds can increase phosphate sorption to soil by forming metal bridges (Borie and Zunino 1983; Levesque and Schnitze 1967). However, phosphate sorbed through organic-metal bonds is thought to be more readily available to organisms than phosphate sorbed to metal-oxides (Gerke 2010).

In soils with abundant iron and aluminum oxide content, phosphate sorption will largely be through ligand exchange reactions and is therefore predicted to be only weakly pH dependent (Sollins et al. 1988), with any effect being in the direction of phosphate sorption decreasing with increased soil pH (McBride 1994). This prediction has been supported for pure

iron oxides (Hingston et al. 1967; Barrow et al. 1980) but non-linear responses, which often have sorption plateaus between pH 4 and 6, have been reported for aluminum oxides (Chen et al. 1973; He et al. 1997). There is also some evidence that when pH effects do influence phosphate sorption, effects may be concentration dependent and absent under low solution phosphate concentrations (Eze and Loganathan 1990), which are typical of forest systems. We therefore predict that any long-term litter input effects on soil pH will have little to no influence on phosphate sorption in this study. For leachate pulses we suspect soil may buffer against leachate pH values (i.e., the pH of an added solution may quickly change to reflect the pH of the soil; Sollins et al. 1988).

Ionic strength of soil solution may be altered by either long-term litter inputs or leachate pulses. Ionic strength has been hypothesized to have little influence on specific-sorption of phosphate because these reactions are largely controlled by ligand exchange and not by electrostatic attraction (Goldberg and Sposito 1984; Sparks 1995). However, increased ionic strength has sometimes been reported to increase phosphate sorption (Edzwald et al. 1976 and He et al. 1997 using kaolinite; McBride 1997 for goethite; Ryden et al. 1977 with soil) and the magnitude of the effect can be dependent on the ion identity. For example, studies manipulating ionic strength with different ions (but controlling for precipitation reactions) have found that calcium (Ca) had a greater influence on phosphate sorption than potassium (K) or sodium (Na) (Barrow et al. 1980; Pardo et al. 1992), but that the effect of ionic strength and ion identity may be less likely at low phosphate concentrations (Ryden et al. 1977).

As a further consideration, rate of phosphate sorption to soil can decrease as initial phosphate concentration in solution increases (van Riemsdijk et al. 1984). Litter leachates can vary greatly in their phosphate concentrations (Schreeg et al. in press) and phosphate concentrations can therefore act as another factor through which organic matter additions influence phosphate sorption. In addition, the dependence of phosphate sorption on initial phosphate concentration, combined with varying concentrations of phosphate in leachates, make initial phosphate concentration a key covariate to consider when designing experiments that investigate leachate DOC competition for sorption sites (Iyamuremye et al. 1996; Guppy et al. 2005).

In this study we conducted a set of laboratory experiments to evaluate the importance of leaf litter inputs on phosphate sorption in a lowland tropical forest in Panama. We investigated long-term effects of litter inputs through a litter manipulation experiment (the 'field litter manipulation' experiment; Objective 1), short-term effects through litter leachate pulses (the 'leachate pulse' experiment Objectives 2a and 2b), the interaction between short and long-term effects (by comparing leachate pulse effects among the field litter manipulation treatment soils), and predictors of soil phosphate sorption (Objective 3; Table 1). Post-sorption recovery of phosphate in the litter manipulation soils was also investigated (Objective 4). Experiments were based on 1 h incubations and a radioactive phosphate tracer (^{32}P). The use of the radioactive tracer allowed us to study low solution concentrations appropriate for non-fertilized forest systems.

We had two main hypotheses. First, for the field litter manipulation experiment, ^{32}P sorption would decrease with litter addition because previously sorbed organic C would occupy potential sorption sites (Objective 1). Secondly, in the leachate pulse experiment, litter leachate would reduce ^{32}P soil sorption relative to a throughfall control because leachate DOC would compete for phosphate sorption sites (Objective 2a). Because leachates have varying concentrations of phosphate and we expected that soil ^{32}P sorption would decrease with initial solution phosphate concentration, we hypothesized that leachate pulses would continue to show decreased ^{32}P sorption due to DOC competition for sorption sites when initial solution phosphate was controlled for (Objective 2b). For the interaction of short-term and long-term effects, we predicted that the effects of leachate pulses on phosphate sorption would be greatest in the leaf litter removal soil. We evaluated pH, but did not expect it to show clear trends with phosphate sorption and litter treatments. We predicted that any correlation between increased phosphate sorption and increased ionic strength of Ca, magnesium (Mg), K and Na would be weak compared to the influence of C decreasing sorption (Objective 3). When considering the effect of field litter manipulation treatment on strength of phosphate sorption, we hypothesized that more of the sorbed ^{32}P would be readily extractable (Bray 1 extract; Bray and Kurtz 1945) for the litter addition soil (Objective 4). We also examined the effects of solution-to-soil ratios to facilitate comparisons among other studies (Objective 5).

Table 1 Overview of the objectives

	Objective					
	1	2a	2b	3	4	5
Main interest	Evaluate field litter manipulation effects on soil phosphate sorption	Evaluate leachate pulse effects on soil phosphate sorption	Evaluate leachate pulse effects on soil phosphate sorption after accounting for covariance in initial phosphate concentration	Evaluate predictors of soil phosphate sorption	Evaluate field litter manipulation effects on post-sorption recovery of phosphate	Evaluate the effect of solution-to-solution ratios on soil phosphate sorption
Experiment/data source	Field litter manipulation experiment	Leachate pulse experiment		Data from leachate pulse experiment	Bray-1 extracts	Incubations with different solution-to-soil ratios
Solutions added	Throughfall control	Throughfall control and leachates from five species			Throughfall control	Throughfall control
Level of analysis with respect to the litter manipulation soils (i.e., litter addition, control, removal)	Across soils	Within soils		Across and within soils	Across soils	Across soils
Statistical test	ANOVA	ANOVA	ANCOVA	Regression	ANCOVA	Regression

The effects of litter inputs on soil phosphate sorption are evaluated over two time scales: (1) the cumulative effect of long-term litter inputs (i.e., 'field litter manipulation' experiment) and (2) the short-term effect of litter leachate pulses on phosphate sorption (i.e., 'leachate pulse' experiment)

Methods

Leaf litter leachate and soil collection

The study was conducted in the Republic of Panama at the Smithsonian Tropical Research Institute (STRI). Soil was collected in early October 2008 from the Gigante Litter Manipulation project (GLiMP) (Sayer et al. 2006; Sayer and Tanner 2010) where three treatments were initiated in 2003: leaf litter doubled, leaf litter removed and a control. Litter added to the litter addition plots came from the litter removal plots. Soils from these plots represent the levels of our 'field litter manipulation' treatment. The GLiMP soil was formed from a Miocene basalt. The soil has been classified as an Oxisol in USDA Soil Taxonomy from profile pits around the litter manipulation plots, but is also classed as Nitisols and Cambisols (FAO) by Corre et al. (2010). Soil was collected (0–10 cm) from three of the five plots of each treatment, air dried under ambient laboratory temperature and humidity (22 ± 0.5 °C and 55 ± 5 %, respectively; air drying

was initiated the same day as collection). Soil was sieved (2 mm), bulked by treatment and stored in plastic bags. Subsamples were dried at 105 °C for 24 h to determine air to oven dry weight conversions. Total soil C was determined by removing all visible organic fragments remaining after the 2 mm sieve, grinding soil in a ball mill and analyzing on an Elemental Analyzer (Flash EA 1112, Thermo, Bremen, Germany).

Freshly senesced leaves of five species (*Albizia guachapele*, *Anacardium excelsum*, *Cecropia peltata*, *Castilla elastica*, *Ficus insipida*) were collected from the forest canopy using the crane in Parque Metropolitano, a seasonal forest with 1,740 mm mean annual precipitation. All five species have large geographical distributions within the neotropics (Croat 1978). *A. excelsum*, *C. peltata* and *C. elastica* are distributed across a range of precipitation levels, while *F. insipida* and *A. guachapele* are mostly restricted to moist forests (Croat 1978). Leaves were collected when they could be removed by a light touch, meaning the abscission zone had formed, leaves

had senesced and were ready to fall. Litter was transported in paper bags and then spread out in thin layers to air-dry under ambient laboratory temperature and humidity (22 ± 0.5 °C and 55 ± 5 %, respectively) for approximately 3 weeks. For each species, senesced leaves were collected from at least three individual trees. Litter was cut when necessary so the maximum size was approximately 5 cm $\times$ 5 cm and samples were bulked at the end of the collecting period (August–October 2008).

Leaf litter leachates, which represent our 'leachate pulse' treatment (Objective 2a and 2b), were created using a 1:30 litter to deionized water ratio based on grams oven dried weight equivalent (ODW). Litter was shaken at low speed (approximately 180 rpm) for 4 h with 250 mL deionized water in wide mouth bottles. Solutions were immediately decanted and centrifuged at $8,180 \times g$ for 10 min. Leachates were made throughout the duration of the experiment and were stored at 4 °C for 1–5 days. All solutions were brought to room temperature before use in the sorption experiments. Solutions were analyzed for molybdate reactive phosphate (MRP; Hach DR 5000 UV–vis spectrophotometer), DOC (Shimadzu TOC-V$_{CSH}$ Total Organic Carbon analyzer), and pH (Hach Sension 3 pH meter). Samples for DOC analysis were prepared (i.e., diluted and acidified) at the time of the phosphate sorption experiment. Cation concentrations were determined by inductively-coupled plasma optical-emission spectrometry (ICP-OES; Optima 2100, Perkin Elmer, Shelton, CT). Ionic strength due to base cations (Ca, K, Mg and Na) was calculated using the formula: $I = 0.5 \sum c_i * Z_i^2$, where Z_i is the valence of the ion and c_i is the ion concentration in mol L^{-1}. Scans of specific ultraviolet absorption (SUVA), which is the measured absorbance divided by the C concentration and expressed here as L g^{-1} C cm^{-1}, were used as an index of C chemistry (Jaffrain et al. 2007; Hur and Schlautman 2003) and measured on the diluted DOC samples (Hach DR 5000 UV–vis spectrophotometer).

^{32}P-phosphate sorption

The effects of field litter manipulation (Objective 1) and species-specific leachate pulses (Objective 2a and 2b) on phosphate sorption were evaluated with carrier free ^{32}P sorption experiments in November and December 2008. The control was a simulated 'throughfall', which was created using nutrient concentrations and ratios from a review on throughfall in lowland tropical forests (Zimmermann et al. 2007; concentrations in Table 3). Within each soil, each species-specific leachate pulse replicate was an independently created leachate using the bulked litter. Three replicates were included per species. In order to control for the role of phosphate on the effects of leachate addition, four levels of phosphate additions were included for throughfall controls (+0, 3, 6, 9, 12 µg mL^{-1}) and the leachates (+0, 2, 4, 6, 8 µg mL^{-1}) so initial phosphate in solution could be used as a covariate.

In batches of 10 samples, 3 mL of DI water was added to 5 g of air-dried soil (which is 4.66 g oven-dried weight) to mimic approximately 60 % gravimetric water content. Sodium azide (1 mM final concentration) was included to inhibit microbial activity (Feuillade and Dorioz 1992). Thirty minutes later leachate, or throughfall control solution, phosphate (^{31}P) and the ^{32}P radioactive isotope tracer were added. Phosphate stock additions (made from dipotassium phosphate) ranged from 0 to 250 µL depending on the target concentration. Leachate, or throughfall control, solutions therefore ranged from 6.75 to 6.50 ml (with the contribution to ^{31}P-phosphate in solution calculated accordingly). The ^{32}P radioactive isotope tracer (0.25 mL of approximately 4 Mdpm per sample) was then added, for a total solution-to-soil ratio of 10 mL to 4.66 g ODW, and samples were shaken on low (180 rpm) for an hour. Additions of the small quantities of radioactive ^{32}P tracer used in this study did not have any appreciable effect on solution phosphate concentration. After centrifuging for 10 min at $8,180 \times g$, supernatant was immediately decanted.

Activity of ^{32}P remaining in the supernatant was determined using a liquid scintillation counter (Beckman Coulter LS 6500 Multipurpose Scintillation Counter, Fullerton, CA) and Ultima Gold AB cocktail. Activities of samples for determining batch-specific ^{32}P tracer additions and blanks were also determined. Subsamples of supernatant were diluted, acidified and frozen for later analysis of DOC (see above).

In addition, for the throughfall control samples, Bray 1 extractable (Bray and Kurtz 1945) ^{32}P was measured to provide insight into how ^{32}P was partitioned among soil sorption pools (Objective 4). Bray 1 extract is a weakly acidic ammonium fluoride solution (0.025 N HCl and 0.03 N NH$_4$F) that serves

as an index of readily extractable orthophosphate (Bray and Kurtz 1945; Kuo 1996). For this analysis, immediately after centrifuging and decanting the supernatant, a clean spatula was used to break up compressed soil in each centrifuge tube. Bray 1 extract was added (for a solution-to-soil ratio of 35 mL to 4.66 g ODW soil), samples were shaken five minutes and centrifuged at $8,180 \times g$ for 15 min. The Bray 1 supernatant was then immediately analyzed for ^{32}P activity (see above).

The effect of solution-to-soil ratio on ^{32}P sorption was investigated using a small number of samples with deionized water (Objective 5). This experiment was carried out in June 2009 using the same bulked soil as used in the above experiments, but a slightly different protocol was followed. This experiment is included here to consider the dependency of percent ^{32}P soil sorption on the solution-to-soil ratios and to determine if the slope of the relationship varies among soil, which is helpful for comparing the results presented here to other work. Total solution was 7.5 mL, as opposed to 10 mL, and the step involving incubation with DI was eliminated. The total solution consisted of 7 mL of the throughfall control, 0.25 mL DI and 0.25 ml ^{32}P, all added at the same time. Also, samples were shaken on the high setting (280 oscillations per minute), instead of low (180 oscillations per minute).

Analysis

The effect of field litter manipulation on the proportion (%) of ^{32}P removed from solution was statistically analyzed using a one-way ANOVA (Objective 1; only the samples that did not receive a ^{31}P-phosphate additions were used in this analysis). To evaluate the effect of leachate pulses on %[32]P sorption, we used two approaches (Objective 2a and 2b). For both approaches, only effects within a soil treatment were analyzed and comparisons were made between each species and the throughfall control. The effect of leachate pulse on %[32]P sorbed was investigated using a one-way ANOVA without controlling for initial phosphate in solution (Objective 2a). The analysis used samples that did not receive ^{31}P-phosphate additions. Differences between the throughfall control and the leachates were evaluated using Dunnett multiple comparison tests. We then evaluated if leachate additions influenced ^{32}P sorption, as compared to a throughfall control, while controlling for initial phosphate in solution (Objective 2b). This was accomplished by including samples that received additions of ^{31}P-phosphate and using an ANCOVA. For ANCOVA, a mixed effects model was used with the solution replicates set as a random effect. This accounted for the fact that initial phosphate concentrations were created by adding ^{31}P-phosphate to subsamples of three replicates for each leachate. Slopes were tested for homogeneity. ANCOVA was done within each soil from the field litter manipulation treatments (i.e., litter addition, control, litter removal). Dunnett multiple comparison tests were used to evaluate differences between the throughfall control and the leachates.

Effect sizes of leachate on phosphate sorption compared to the throughfall control were calculated using Cohen's d statistic (Cohen 1988). The initial phosphate in solution was controlled for by using the intercepts from the ANCOVA where initial ^{31}P-phosphate in solution was the covariate: Cohen's d = (intercept of %[32]P sorbed with throughfall control − intercept of %[32]P sorbed with leachate)/ pooled standard deviation.

The intercepts of %[32]P sorbed were also used in simple linear regressions within each soil to investigate the trends between phosphate sorption and initial pH, net DOC sorbed and ionic strength due to Ca, K, Mg and Na while controlling for solution phosphate concentration (Objective 3). Net DOC sorbed was calculated as the DOC in the initial solution minus that of the final solution. Species differences in leachate $SUVA_{254}$ were evaluated using an ANOVA and multiple comparisons were investigated with a Tukey test. When data are summarized as ratios of leachate to throughfall control effects, absolute standard deviations were calculated using propagation of uncertainty for ratio functions (Ku 1966).

For Bray 1 extraction to evaluate post-sorption recover of [32]P (Objective 4), the overall effect of soil type was investigated using ANCOVA with initial phosphate in solution as a covariate, which was appropriate because slopes among soils were not found to differ significantly. For the solution-to-soil ratio experiment (Objective 5), soil effects on slopes of the %[32]P sorbed as a function of solution-to-soil ratio were evaluated using t-tests after a linear model was fit for each soil. All statistical analyses were conducted in R (R Development Core Team 2012).

Results

Soil C content and leachate characteristics

The leaf litter addition soil contained 3.8 % total soil C, while the control soil contained 3.2 % and the litter removal was 2.8 % (Table 2). Resin extractable phosphate and pH also showed trends related to the litter treatment (Table 2). Resin extractable phosphate quantifies the pool of phosphate that is easily removed by solution disequilibrium (Sato and Comerford 2006). Leachates varied in initial concentrations of DOC

(240–1,053 mg C L^{-1}), phosphate (0.81–6.4 mg L^{-1}) and cations (Table 3).

Effect of field litter manipulation on phosphate sorption (Objective 1)

Litter addition soil sorbed less phosphate during the 1 h incubation than the litter removal and control soil, and all soil comparisons were significantly different from one another (Fig. 1). Although differences were small when considered on a percent sorbed basis, with all soils sorbing more than 99 % of the added tracer, the relative differences of phosphate remaining in solution were large. For the litter addition soil, five-fold more phosphate remained in solution compared to the litter removal soil, and two-fold more phosphate remained in solution at the end of the 1 h incubation compared to the control soil.

Effect of leachate pulses on phosphate sorption (Objectives 2a, 2b, 3)

Leachates of all species decreased phosphate sorption in the litter removal soil when compared to the throughfall control (Objective 2a; Table 4). This was also true when ^{31}P-phosphate was added to control for initial phosphate concentrations in solution (analyzed using an ANCOVA; Objective 2b; Table 5; Fig. 2), demonstrating that some leachate property or properties, besides differences in initial phosphate in

Table 2 Characteristics of the Gigante Litter Manipulation project (GLiMP) soils (0–10 cm), which we refer to as 'field litter manipulation' treatments

	Litter treatment		
	Removal	Control	Addition
%C*	2.8 (0.3)	3.2 (0.1)	3.8 (0.5)
Total P (mg kg^{-1} soil)	262.3 (13.2)	285.6 (17.8)	266.4 (28.1)
Resin P (mg kg^{-1} soil)	0.47 (0.16)	0.51 (0.14)	0.95 (0.02)
pH (in water)	5.04 (0.15)	5.19 (0.31)	5.78 (0.01)

Soil for this study was collected in October and November 2008 and %C was measured on the soils that were bulked and used in this study (indicated by *). All other values are for soils collected in January 2009 from the same GLiMP plots used in this study (BL Turner, unpublished data). Means ± standard deviations are based on two plots per litter treatment

Table 3 Characteristics of leachate and the simulated throughfall control

	A. gauchabele	A. excelsum	C. elastica	C. peltata	F. insipida	Throughfall control
pH	5.06 (0.04)	4.97 (0.07)	6.16 (0.02)	7.05 (0.76)	7.72 (0.11)	5.5
DOC (mg L^{-1})	240.1 (38.9)	1053.6 (76.9)	785.1 (29.4)	533.5 (38.2)	631.7 (51.7)	8.2
Phosphate-P	4.80 (0.28)	6.43 (0.48)	6.13 (0.33)	2.95 (0.20)	0.81 (0.18)	0.03
Al	<LOD	<LOD	<LOD	<LOD	0.530 (0.121)	
Ca	8.35 (1.11)	7.15 (1.88)	127.30 (11.84)	82.51 (18.41)	128.24 (4.25)	0.4
Mg	8.60 (0.82)	112.78 (1.54)	91.63 (10.59)	36.83 (8.12)	65.39 (4.40)	0.24
K	178.53 (8.95)	120.81 (8.94)	381.91 (48.03)	487.93 (23.39)	173.20 (9.88)	1.99
Mn	0.31 (0.06)	0.09 (0.01)	0.17 (0.03)	0.03 (0.01)	0.02 (0.01)	
Na	0.43 (0.02)	4.04 (0.26)	3.84 (0.75)	2.17 (0.10)	3.92 (0.14)	0.46
Si	0.28 (0.05)	4.67 (0.02)	6.72 (0.68)	8.63 (2.55)	12.74 (0.73)	

All values, except pH, are mg L^{-1}. Phosphate-P is reported as molybdate reactive phosphate (MRP). Means and standard deviations (in parentheses) are for the original leachate solutions made using a 1:30 litter-to-solution ratio and 4 h extract time ($n = 3$, with the exception of throughfall control). Leachates and throughfall control were then diluted with deionized water for the sorption experiments (i.e., 6.75 ml of leachate in 10 ml total solution for the samples without ^{31}P-phosphate additions; see methods). Values lower than the limit of detection are indicated by <LOD
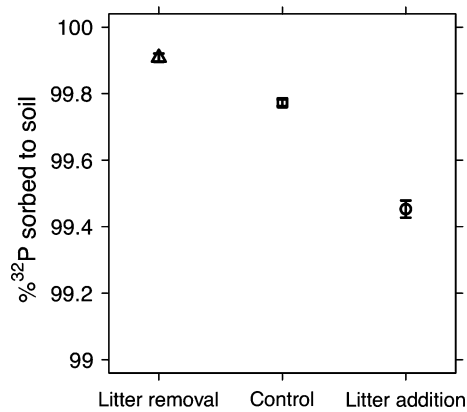
Fig. 1 The effect of field litter additions on phosphate-^{32}P sorption to soil during a 1 h incubation with the throughfall control solution. Bars show standard deviations of $n = 3$ replicates. All soil comparisons are significantly different from one another ($P < 0.05$) as evaluated using a one-way ANOVA and Tukey multiple comparisons

solution, underlie the decreased phosphate sorption. In the control soil, fewer species had a significant effect on decreasing phosphate sorption. In the litter addition soil one species, *A. excelsum*, increased phosphate sorption (Table 5; Fig. 2). Although the differences between the throughfall control and leachate were small, the increase in phosphate remaining in solution for the leachate treatments relative to the throughfall control was greater by a factor of two for some species in the litter removal and control soils (Fig. 3).

In the ANCOVA (Objective 2b), there were two cases where slopes were not homogenous with the slope of the throughfall control for the respective field litter manipulation soil (*Castilla elastica* in control soil and *Anacardium excelsum* in addition soil); however, in both cases leachate slopes converged with that of the throughfall control solution as the functions approached the intercept. Thus, the difference between treatments will be even greater at larger values of the covariate (i.e., initial phosphate in solution) than at the intercept. An assessment of treatment differences at the intercept is therefore conservative, and appropriate, for evaluating significance in these two cases.

Linear regressions showed leachate pH and net DOC sorbed were not significant predictors of phosphate sorption for any of the soils (Objective 3; Table 6). Contrary to expectations, the combined ionic strength of Ca, K, Mg and Na was strongly negatively correlated with phosphate sorption in the litter removal soil (Table 6).

When considering all soils together, the effect of leachate on reducing %^{32}P sorption increased as net DOC sorbed increased (Fig. 4) for four of the species investigated. However, *A. excelsum* did not fit this trend. *A. excelsum* shows the largest net DOC sorbed and one of the lowest effects of leachate on decreasing phosphate sorption in the litter removal soil, in addition to showing increased phosphate sorption

Table 4 ANOVA and Tukey multiple comparison results for the effect of solution (i.e., species leachate and throughfall control) on ^{32}P-phosphate sorption to soil

	Soil litter treatment		
	Removal	Control	Addition
F-value	113.7	18.9	73.0
P value	<0.0001	<0.0001	<0.0001
%^{32}P sorbed			
A. gauchabele	99.831 (0.014)*	99.686 (0.074)*	99.297 (0.031)*
A. excelsum	99.809 (0.012)*	99.733 (0.027)	99.498 (0.013)
C. elastica	99.605 (0.026)*	99.491 (0.026)*	99.131 (0.017)*
C. peltata	99.803 (0.019)*	99.692 (0.032)*	99.384 (0.009)*
F. insipida	99.789 (0.004)*	99.685 (0.032)*	99.364 (0.045)*
Throughfall control	99.908 (0.013)	99.772 (0.010)	99.453 (0.026)

Analyses were done within a soil treatment (df = 5, 12). Means of %^{32}P sorbed to soil are included and standard deviations are shown in parentheses. Asterisks indicate if the species leachate was significantly different from the throughfall control, as determined through the Dunnett multiple comparison tests. Leachates varied in their initial phosphate concentrations (Table 3) and covariance of %^{32}P sorption with the initial solution phosphate concentration is not controlled for in this analysis (see Table 5 for ANCOVA)

Table 5 Species-specific leachate effects on ^{32}P-phosphate sorption compared to a throughfall control using ANCOVA, with initial phosphate in solution as a covariate, and Dunnet multiple comparison tests

Soil	Solution	Diff %^{32}P	z-value	P value	Cohen's d
Litter removal	*A. gauchabele*	0.054	−8.087	<0.0001	2.80
	A. excelsum	0.054	−8.046	<0.0001	2.93
	C. elastica	0.275	−40.83	<0.0001	11.11
	C. peltata	0.100	−15.17	<0.0001	4.73
	F. insipida	0.123	−18.46	<0.0001	7.43
Control	*A. gauchabele*	0.032	−2.39	0.052	0.75
	A. excelsum	−0.017	1.26	0.454	−0.39
	C. elastica	0.247	−18.29	<0.001	5.68
	C. peltata	0.063	−4.72	<0.001	1.52
	F. insipida	0.079	−5.90	<0.001	1.95
Litter addition	*A. gauchabele*	0.044	−2.02	0.150	0.58
	A. excelsum	−0.208	9.40	<0.001	−2.64
	C. elastica	0.237	−10.75	<0.001	3.03
	C. peltata	0.012	−0.54	0.971	0.16
	F. insipida	0.093	−3.01	<0.001	1.32

Analyses were conducted within each soil type

Differences in the percent of ^{32}P sorbed (diff %^{32}P) were calculated as the mean %^{32}P sorbed in the presence of species-specific leachate minus that of throughfall control at the y-intercept of the ANCOVA. The P values were determined by a Dunnett test and indicate if leachate differed significantly from the throughfall control. Degrees of freedom are 5, 78 for the ANCOVA within each soil. Effect size is reported as Cohen's d, which is the difference between the means (i.e., diff %^{32}P) divided by the pooled standard deviation

with leachate presence in the litter addition soil (Fig. 4).

Effect of soil treatment on Bray 1 extractable ^{32}P (Objective 4)

Less than 10 % of the ^{32}P sorbed during a 1 h incubation with the throughfall control was desorbed by the subsequent Bray 1 extraction (Fig. 5). However, the percent extracted from the litter addition soil was 40 % greater than that extracted from the control and litter removal soil. The recovery of the ^{32}P in the Bray 1 extract across soil treatments serves as an index of litter influences on phosphate desorption and suggests that plant availability of sorbed phosphate increases with litter addition.

Solution-to-soil ratios (Objective 5)

The solution-to-soil ratio used for the 1 h incubations was found to have a strong effect on the percent of the initial ^{32}P sorbed. For example, in the litter addition soil, the percent of ^{32}P remaining in solution varied from 99.75 to 98.25 %, with a greater percent of the phosphate tracer sorbed when there was less solution per gram of soil. Furthermore, the effect of the solution-to-soil ratio on phosphate sorption differs among litter manipulation treatments. The effect is greater for the litter addition soil than for the control and litter removal soil, as shown by slopes for the response of ^{32}P sorbed as a function of solution-to-soil ratio (Fig. 6).

SUVA of leachate—*A. excelsum* had significantly higher SUVA$_{254}$ than leachates of the other species, while the other species were not significantly different from one another (Fig. 7; $P < 0.001$ for ANOVA, df = 4,10; $P < 0.002$ for all *A. excelsum* Tukey comparisons with other species).

Discussion

This laboratory study demonstrates that leaf litter inputs can reduce phosphate sorption to soil through both long-term inputs in the field and short-term litter leachate pulses. The field litter addition treatment resulted in soil that sorbed significantly less phosphate

Fig. 2 Leachate effects on reducing phosphate-^{32}P sorption to soil during a 1 h incubation. See Table 5 for a summary of leachates that significantly influenced phosphate sorption compared to the throughfall control. On the *x*-axis, 'initial ^{31}P-phosphate in solution' refers to the molybdate reactive phosphate in the unaltered leachate or throughfall solution, plus any ^{31}P-phosphate that was added to the solution in order to create a range of initial phosphate concentrations. For the throughfall control solution, covariance relationships with initial phosphate in solution were: $Y = 99.479 - 0.036 * x$ (Litter addition soil); $Y = 99.774 - 0.012 * x$ (control soil); $Y = 99.910 - 0.009 * x$ (litter removal soil)
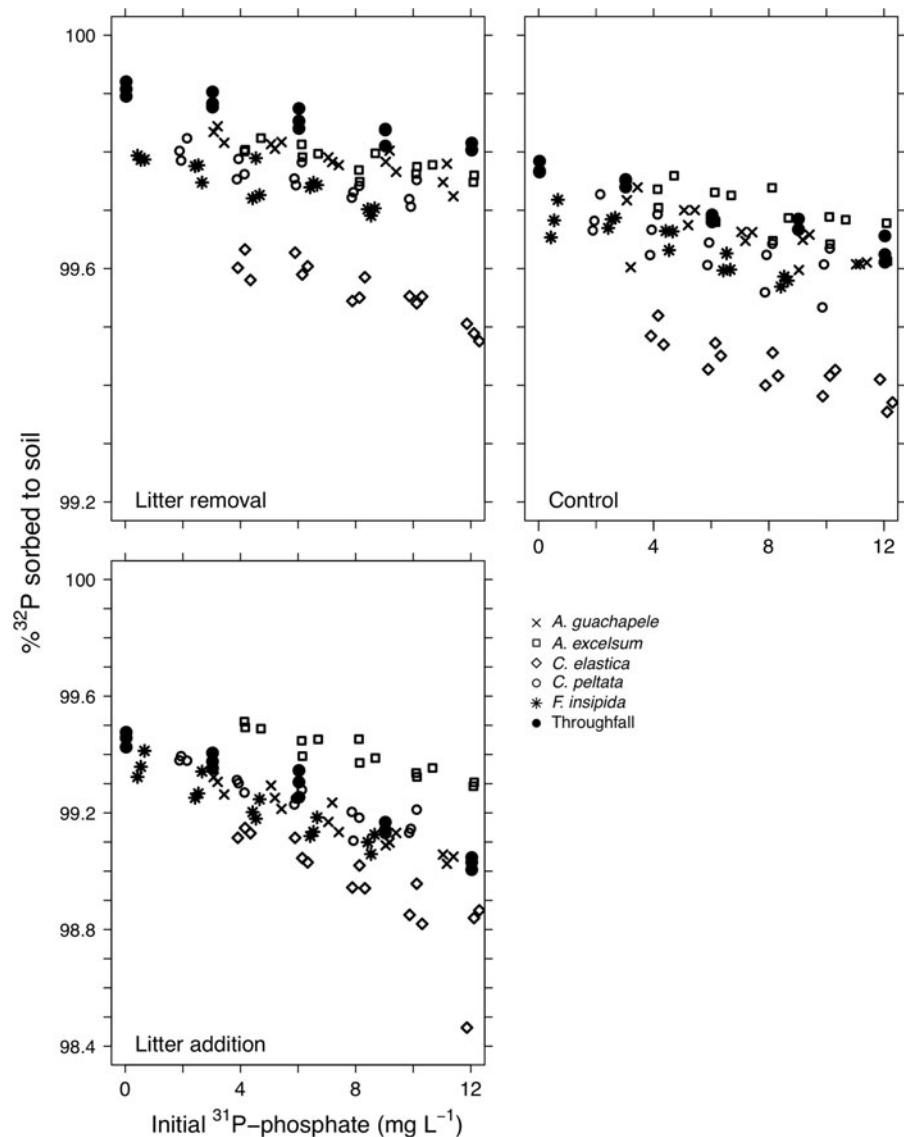
and maintained five-fold more phosphate in solution compared to the litter removal soil at the end of 1 h incubations (Fig. 1). We note that this relative difference can change with solution-to-soil ratio under the non-equilibrium conditions of this experiment (Fig. 6). Results presented here would have appeared greater if we had used a less concentrated ratio, such as a 10 or 40 mL solution to 1 g of soil, which is common in many soil sorption experiments (Bache and Williams 1971; Juo and Fox 1977).

Leachate pulses from all five species decreased phosphate sorption to the litter removal soil, showing that leachate pulses are another avenue by which organic matter inputs can influence P cycling. Interestingly,

leachate pulses had a greater effect on decreasing phosphate sorption in the long-term litter removal soil than the litter addition and control soil (Fig. 3; Table 5). This interaction demonstrates that the effects of leachate pulses are sensitive to previous inputs of organic matter and, because field litter inputs attenuated the effect of the leachate pulse, it is likely that mechanisms by which field litter manipulations and leachate pulses are controlling phosphate sorption are similar.

Mechanisms underlying phosphate sorption results

For the field litter manipulation study, litter removal soil was found to have much greater phosphate
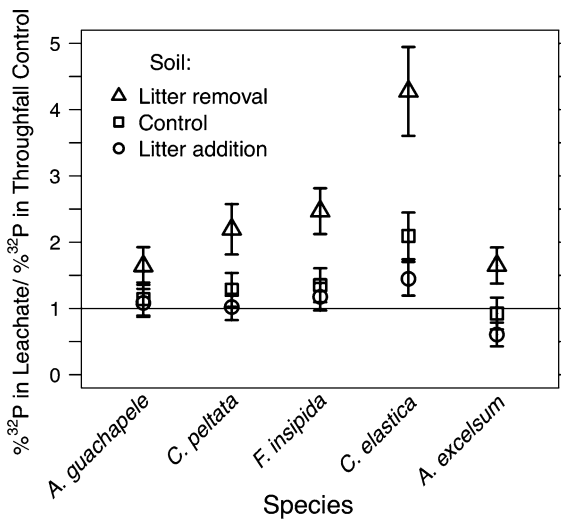
Fig. 3 The difference in ^{32}P-phosphate in supernatant of leachate relative to the throughfall control, calculated as %[32]P in leachate supernatant/%[32]P in th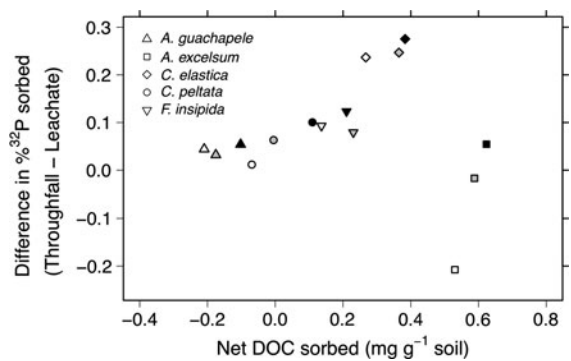roughfall control supernatant. *Bars* show absolute standard deviations calculated using the propagation of uncertainty for a ratio (see "Methods" section)

Fig. 4 Relationship between leachate effect on phosphate-^{32}P sorption and net dissolved organic carbon sorption to soil. *Black symbols* are for litter removal soil, *grey symbols* show control soil and *open symbols* represent litter addition soil

sorption than the control and litter addition soil. As outlined previously, phosphate sorption in non-equilibrium conditions is a function of solution phosphate concentration. The litter addition soil, however, likely had a greater phosphate concentration in the soil prior to the addition of any experimental solution. Therefore, the extent that soil solution phosphate concentration underlies the ^{32}P sorption results deserves consideration. Using the relationships of initial phosphate concentration on %[32]P sorption (Fig. 2) and

water extractable phosphate between the litter removal and addition soil (0.2 µg P mL^{-1} or 0.4 µg P g^{-1} soil; Schreeg unpublished data) we calculate that the difference in soil solution phosphate concentration prior to addition of experimental solutions is expected to influence %[32]P sorption by less than 0.008 percentage points (here we use percentage points to clarify that we are referring to an absolute differences between the %[32]P results rather than a relative change, or a percent calculated from the %[32]P values). This is much less than the observed 0.43 percentage points between the litter addition and removal soil (0.52 %, compared to 0.09 %) we therefore conclude that the difference in %[32]P sorption among the field litter manipulation soils is due to more than a difference in solution phosphate concentrations. In the leachate

Table 6 Simple linear regressions evaluating pH, ionic strength (based on Ca, K, Mg and Na) and net DOC sorbed as predictors of %[32]P sorbed to soil

Soil litter treatment	Intercepts of %[32]P sorbed as a function of	Slope	r^2	*P*-value
Addition	Leachate pH	−0.059	0.21	0.363
	Ca, K, Mg, Na ionic strength	−0.011	0.14	0.461
	Net DOC sorbed	0.125	0.07	0.720
Control	Leachate pH	−0.032	0.14	0.466
	Ca, K, Mg, Na ionic strength	−0.014	0.52	0.108
	Net DOC sorbed	−0.076	0.06	0.632
Removal	Leachate pH	−0.033	0.15	0.433
	Ca, K, Mg, Na ionic strength	−0.017	0.73	**0.030**
	Net DOC sorbed	−0.144	0.20	0.368

The intercepts from the ANCOVA of %[32]P sorbed to soil, where initial phosphate in solution was a covariate, were used as the response variable. Net sorbed DOC is DOC initially in solution minus DOC remaining in supernatant at end of 1 h incubation. Significant correlations are in bold. All models have 5 degrees of freedom
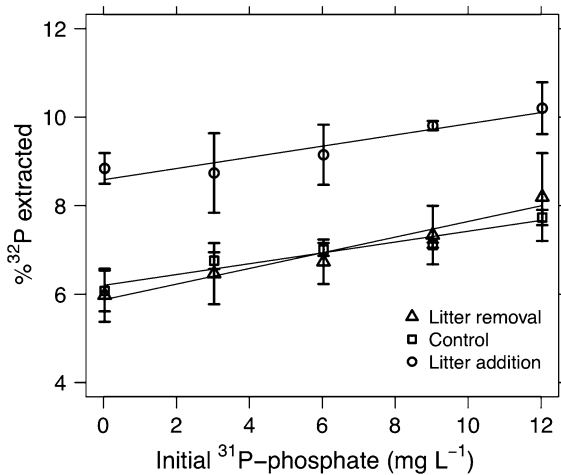
Fig. 5 The percent of sorbed ^{32}P-phosphate that was subsequently extractable in Bray 1 solution. Bray 1 solution was added after a 1 h incubation with throughfall control solution. *Bars* show standard deviation. On the *x*-axis, 'initial ^{31}P-phosphate in solution' refers to the molybdate reactive phosphate in the unaltered leachate or throughfall solution, plus any ^{31}P-phosphate that was added to the solution in order to create a range of initial phosphate concentrations. Note the *x*-axis does not extend to zero. ANCOVA of the intercepts showed the litter addition had significantly greater extractable ^{32}P than the litter removal or control soil at the $P = 0.05$ level
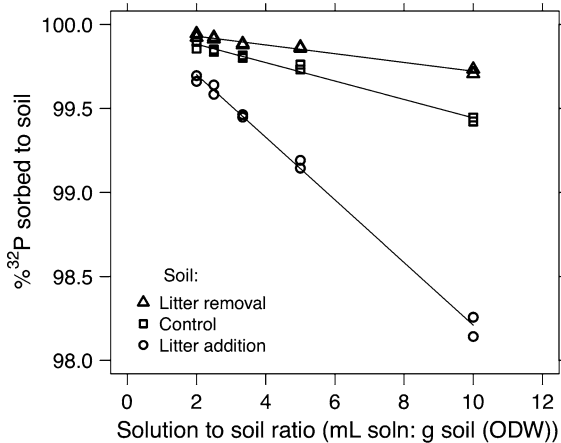

Fig. 6 The effect of solution-to-soil ratios on phosphate sorption for the three field litter manipulation soils. All samples had 7.5 ml total solution and were shaken at 280 oscillations per minute. Data points show two analytical replicates of each bulked soil. Litter addition soil: $y = 100.07 - 0.186 * x$, $r^2 = 0.996$; control soil: $y = 99.99 - 0.0548 * x$, $r^2 = 0.985$; litter removal soil: $y = 99.98 - 0.0261 * x$, $r^2 = 0.977$. *T* tests showed slopes of all soils were significantly different at the $P = 0.05$ level
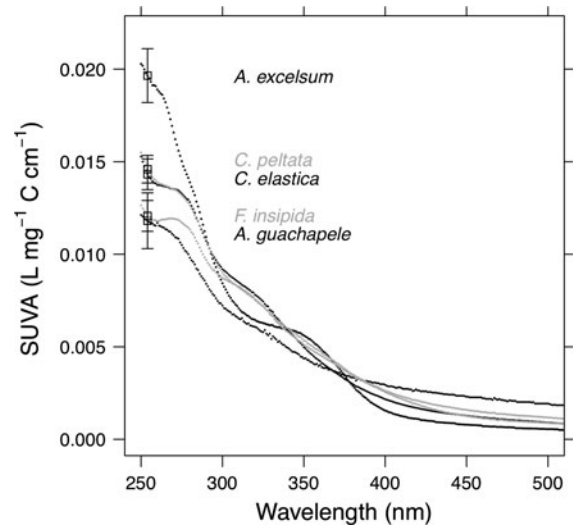
Fig. 7 SUVA wavelength scans of initial leachates (averaged from three replicates). Standard deviations are shown for SUVA at 254 nm

pulse experiments we were able to determine through an analysis of covariance that the leachate effect was due to more than an increase in solution phosphate concentration (Fig. 2).

Some variable, in addition to phosphate concentration, must therefore underlie the litter treatment effect. Linear regressions for the leachate pulse experiment suggest that pH is not a significant predictor of leachate pulse effect on phosphate sorption (Table 6). In the litter removal soil, ionic strength (as evaluated by considering Ca, Mg, K and Na) was negatively correlated with phosphate sorption to soil, yet previous research suggests increased ionic strength of these ions should increase or have little influence on phosphate sorption (Ryden et al. 1977; Sparks 1995). Given that three of the leachates had pH values >6 (Table 3), and that Ca makes a large contribution to ionic strength due to its valence charge, the possibility of Ca-phosphate precipitation deserves mention (Barrow et al. 1980). Calcium phosphate precipitation seems unlikely given that this soil buffers against initial solution pH. This was determined by noting that final supernatant pH values were similar, reflecting that of the soil after the hour incubation (determined using the control soil and solutions with initial pH ranging from 4.5 to 7.9; data not shown). Furthermore, Ca-phosphate precipitation would decrease phosphate in solution, which would be interpreted in this study as

increased sorption with increasing Ca concentration. The observed trend is the opposite of this expectation. Mechanisms underlying the correlation of decreased phosphate sorption with increased ionic strength of Ca, K, Mg and Na in the litter removal soil therefore remain unknown. We note that decreased activity coefficients (which would be expected with increased ionic strength) have been suggested, but were not supported, as a potential mechanism decreasing phosphate sorption (Bar-Yosef et al. 1988). Given the results of this study, investigation of the relationship between activity coefficients and phosphate sorption may be an avenue for future work.

Across soils, net DOC sorption was correlated with the difference in ^{32}P sorption between leachate and throughfall control, with the exception of A. excelsum (Fig. 4). However, within each soil from the field litter manipulation treatments, we did not find a significant relationship between net DOC sorbed and ^{32}P sorption (Table 6). Due to the low sample size of these regressions ($n = 6$), we did not test for a relationship after removing A. excelsum. A more robust analysis using a metric of the difference in $\%^{32}P$ sorbed between the throughfall control and leachate to compare how phosphate sorption varies with net DOC sorption across soils (Fig. 4) suggests the A. excelsum could be driving the lack of a relationship between net DOC sorption and ^{32}P sorption when evaluated within a soil (Table 6). This may not be surprising because it is known DOC chemistry can underlie preferential sorption of DOC compounds to different soil sorption sites and not all DOC that is sorbed can compete with phosphate for sorption sites (Kafkafi et al. 1988; Yuan 1980). Furthermore, species leachates differ in DOC chemistry (Hongve et al. 2008). It is therefore likely that net DOC sorbed will provide only coarse scale information on the role of DOC on phosphate sorption.

Information on specific ultraviolet absorption (SUVA$_{254}$), an index of C aromaticity (Hur and Schlautman 2003), provides insight in the absence of detailed information on leachate chemistry. Leachate of A. excelsum was the only leachate found to increase phosphate sorption (which occurred in the litter addition soil) and also had greater SUVA$_{254}$ compared to the other four species (Fig. 7). In some cases, high molecular weight aromatic organic decomposition products, such as humic and fulvic acids, have been suggested to increase phosphate sorption by forming new sorption sites for phosphate (Appelt et al. 1975; Gerke 2010; Levesque and Schnitze 1967). Although C in the A. excelsum leachate from fresh litter would not be a decomposition product, the aromaticity could be related to the increased phosphate sorption when leachate from A. excelsum litter was added to the litter addition soil. Continuing with this speculation, A. excelsum leachate could have similarly sorbed phosphate through organic–metal bridges in the litter removal soil; however, sorption of phosphate through this pathway may have had a small effect relative to the competition of other forms of C with phosphate for sorption sites, resulting in a net decrease in phosphate sorption compared to the throughfall control. It is important to note that in contrast to specific sorption to soil, phosphate sorbed to organic matter is considered more plant available (Gerke 2010; Harter 1969).

Our results for Bray 1 extractable ^{32}P in the field litter manipulation soils demonstrate that litter additions can decrease the strength of phosphate sorption. Sorbed ^{32}P-phosphate in the litter addition soil was more readily extracted than ^{32}P sorbed in the control and litter removal soil (Fig. 5). Other studies report that organic matter additions can increase the fraction of phosphate going to non-specific sorption pools (Easterwood and Sartain 1990; Sharpley and Smith 1989). As mentioned above, one mechanism for this is phosphate sorbed through organic–metal bonds (Gerke 2010). Furthermore, a positive correlation between soil C and readily extractable phosphate has been shown for a number of systems (Harter 1969; Johnson et al. 2003). Our results show that the strength of phosphate sorption may be manipulated by organic matter inputs and supports the proposed link between readily extractable P and soil C concentrations.

Leachate concentrations

The DOC concentrations used here (162–710 mg C L^{-1}) are within the range of field data when biases of collection methods and differences in litterfall quantity between systems are considered. For example, DOC concentrations of field leachates of fresh litter in a spruce stand in Norway were 170 mg C L^{-1} (Froberg et al. 2007, filtered using 0.2 µm pore size, biweekly sampling, no microbial inhibitor noted). Concentrations were 145 mg C L^{-1} in a beech forest and 106 mg C L^{-1} in a pine forest after summer rainstorms (Kaiser et al. 2001, 0.45 µm pore size filters, 7 day

sampling frequency, no microbial inhibitor mentioned). However, lower concentrations of 70 mg L^{-1} were reported for a hardwood stand in Germany (Park and Matzner 2003, 0.45 μm pore size filters, collected biweekly, no microbial inhibitor mentioned) and much lower values have been reported from an oak dominated forest in Appalachia (30 mg L^{-1}, Qualls et al. 1991, GF/F filter, usually sampled after storms, mercuric chloride added if not scheduled to be sampled immediately after storms). Litter inputs in temperate forests are in general much lower than those in seasonal tropical forests (Scott and Binkley 1997; Vitousek 1984), which can directly affect DOC concentration of leachate from fresh litter, because litter thickness can be related to leachate concentration (Park and Matzner 2003). In addition, when comparing among studies, field solutions collected on an infrequent basis may provide low estimates of DOC due to oxidation by microbes if microbial inhibitors were not included. Also, the process of filtering, and the chosen pore size, can reduce total DOC concentrations compared to the non-filtered supernatant values reported in this study. Furthermore, when considering appropriate leachate concentrations for non-equilibrium sorption reactions in laboratory experiments, the soil-to-solution ratio is of importance (Fig. 6). We note that this study used a ratio of 4.66 g soil to 10 ml for the sorption experiments, resulting in less leachate DOC per g of soil compared to the commonly used ratio of 1 g of soil to 10 mL solution.

Biological relevance of results

Phosphate uptake by plants and microbes is from soil solution (Barrow 1978; Oberson and Joner 2005; Syers et al. 2008). In less weathered agricultural soils with high P inputs, P loss via leaching of soil solution P through the soil profile is a concern (Sims et al. 1998; Turner and Haygarth 2000). In contrast, strongly weathered soils tend to sorb phosphate quickly (see Introduction), so P leaching is negligible and factors controlling the low concentrations of phosphate in the soil solution pool (i.e., P that is directly available for biological uptake) are a primary interest. The strongly weathered soil investigated in this study had strong affinity for phosphate, as indicated by >99 % sorption during 1 h incubations. In addition, the sorbed phosphate was largely retained in forms that are not readily available to plants, as determined using Bray 1 extracts (Fig. 5). The magnitude and strength of

phosphate sorption in this strongly weathered soil suggest that any effect of litter on increasing soil solution phosphate could be biologically relevant to meeting plant phosphate demands when the contributions are compounded over annual time periods and extrapolated to larger spatial areas. Therefore, although the differences in percent phosphate sorption are small between litter treatments and controls, even small differences have the potential to be biologically important. We also note that the magnitude of the difference in the percent ^{32}P sorbed between treatments and the control is relative to the solution-to-soil ratio. The magnitude of the effect would have been greater had a more traditional solution-to-soil ratio been used (Fig. 6 and discussion above).

In this study we intentionally isolated the role of physicochemical soil properties on phosphate sorption. In the field, however, microbes can compete with soil sorption sites for phosphate (Oberson and Joner 2005; Olander and Vitousek 2004). It has been hypothesized that efficient microbial competition can in turn increase the bioavailability of P by acting as a biological reservoir, or P holding pool, that is more active than P sorbed to metal oxides in strongly weathered soils (Oberson and Joner 2005). By retaining more phosphate in solution over short time periods, our results suggest that litter, through both long term litter inputs and leachate pulses, may enhance the ability of microbes to compete with soil sorption sites for solution phosphate. Furthermore, we speculate that the abiotic mechanisms investigated in this study may accentuate effects that litter inputs have on increasing microbial P competition for soil solution phosphate. Because soil microbes are often thought to be C limited or co-limited (Wardle 1992; Zak et al. 1994; Allen and Schlesinger 2004), litter leachate rich in DOC can increase microbial activity and/or biomass (Park et al. 2002; Wieder et al. 2008), leading to increases in microbial P demand (Cleveland et al. 2002). In turn, an increase in microbial P demand may increase the ability of microbes to compete with soil sorption for soil solution phosphate (Olander and Vitousek 2004). We hypothesize that physicochemical effects of litter on potentially increasing phosphate availability to microbes may therefore operate concurrently with litter effects on increased microbial uptake of P.

Finally, much work supports the idea that under certain conditions sorbed phosphate in strongly

weathered soils is more readily accessible by microbes than conventionally thought. In anaerobic soil environments, phosphate can be released when iron is used as electron acceptor (Chacon et al. 2006) and it has been suggested that under conditions of high C availability microbes may readily access phosphate from pools traditionally defined as having low availability (Esberg et al. 2010). Such studies emphasize that the relative importance of, and the interactions between, physicochemical and microbial controls on P cycling are likely to vary spatially and temporally.

Conclusions

This study demonstrates that litter inputs can influence both the magnitude and strength of phosphate sorption in a strongly weathered soil over two time scales: long-term litter inputs and short-term leachate pulses. Leachate pulses had a greater influence on decreasing soil phosphate sorption in the field litter removal treatment, and less influence in the field litter addition soil. Long-term litter inputs therefore mitigate the effect of short-term pulses, suggesting that over both litter time scales mechanisms underlying the effect of litter inputs on short-term phosphate sorption may be similar. In addition to decreasing the quantity of phosphate sorbed, we provide evidence that litter inputs can decrease the strength of phosphate sorption. This work adds to the large body of literature showing that organic matter inputs serve as not only a nutrient input to the soil environment but indirectly alter nutrient availability (Berendse 1998; Chapin 1993; Hobbie 1992). While this work focuses on forest litter, our results add support to the claim that litter from crops and agroforestry trees can enhance P availability in low input agricultural systems on strongly weathered soils (Nziguheba et al. 2000). This work also suggests that changes in quantity of forest litter produced, which can occur during early forest succession (Ewel 1976) and which may occur as a response to climate change (Nepstad et al. 2004), could have potential feedbacks to P cycling by altering physicochemical interactions between C, phosphate and soil sorption sites.

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