Phosphorus Sorption Dynamics of Anion Exchange Resin Membranes in Tropical Rain Forest Soils

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Bioavailable P is recognized as a major constraint on productivity in many tropical rain forests. Nevertheless, insufficient knowledge about short-term temporal patterns in soil labile P limits our understanding of the mechanisms controlling soil P supply in tropical forest soils. The use of field-deployed anion exchange resin membranes (AEMs) to determine soil nutrient supply rates is increasingly common, however, the lack of information regarding their behavior over time in tropical wet forest soils interferes with interpretation of results. This study quantifies in situ labile P as measured by AEMs over various incubation periods (4, 8, 12, 14, 20, and 24 d) in the surface soil of two neighboring Costa Rican tropical rain forest Oxisols of differing P content (0.46 vs. 1.18 Mg ha^{-1}, 0–10 cm). Using a nested design, we evaluated the importance of incubation length, environmental conditions (i.e., rainfall, temperature, and solar radiation), vegetation characteristics (i.e., basal area, stem density, and species composition), and total P status in driving spatial and temporal variability in AEM P. Spatially averaged AEM P in the site with higher P content ranged from 0.26 to 1.38 μg membrane^{-1} across all incubation periods; approximately two fold higher than AEM P in the more P-deficient site (0.11–0.77 μg membrane^{-1}). Temporal variability in AEM P was best explained by rainfall. Despite consistently high volumetric soil moisture (50–66%), increasing rainfall was associated with greater P availability in both sites. Mean P availability increased with plant basal area and basal area of legumes.

Abbreviations: AEM, anion exchange resin membrane; DIW, deionized water.

Despite the recognized importance of P cycling to the productivity of tropical rain forests and their potential sensitivity to short-term fluctuations in bioavailable P (Vitousek, 1984), the coarse temporal resolution of P-cycling studies limits our understanding of environmental controls on labile P. Conventional P extractions and lab incubations are not sensitive to the on-site processes that influence P release from decomposing material. The use of AEM incubations to quantify in situ soil nutrient fluxes at fine temporal and spatial scales is becoming more common; however, lack of a standardized method complicates the interpretation of results in a broader context.

Anion exchange resin membranes are thought to be functionally similar to plant roots, acting as sinks for P ions made available by both biological and geochemical release (Menon et al., 1990; Skogley et al., 1990; Yang and Jacobsen, 1990; Walbridge, 1991). However, evidence suggests that in tropical soils with low solution P and high sorption capacity, AEMs act as dynamic exchangers rather than infinite sinks for P (Krause and Ramlal, 1987; Cooperband and Logan, 1994; McGrath et al., 2000; Drohan et al., 2005; Meason and Idol, 2008). The AEMs adsorb anions from solution until an equilibrium is reached, after which they are thought to provide a composite measure of soil labile P that is dependent on soil P sorption capacity, microbial P demand, and the level of plant available P (Cooperband and Logan, 1994; McGrath et al., 2000; Qian and Schoenau, 2002; Drohan et al., 2005; Meason and Idol, 2008). As an equilibrium measure of P bioavailability, AEMs have been used successfully to detect site, environmental, and

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treatment effects in tropical soils (McGrath et al., 2000; Idol et al., 2007; Meason and Idol, 2008).

Previous work investigating climatic controls on P supply in tropical soils has focused on seasonal variation and has emphasized the importance of soil moisture in regulating P availability (Singh et al., 1989; Yavitt et al., 1993; Yavitt and Wright, 1996; Lodge et al., 1994; Campo et al., 1998; McGrath et al., 2000). Strong pulses in nutrient availability, observed at the onset of the rainy season in a number of tropical forests (Singh et al., 1989; Davidson et al., 1993; Lodge et al., 1994; McGrath et al., 2000), have been attributed to the lysis of microbial biomass due to osmotic stress as well as leaching of nutrients from litter accumulated during the dry season (Sparling et al., 1987; Singh et al., 1989; Lodge et al., 1994; Grierson et al., 1998; McGrath et al., 2000). However, few studies have investigated fluctuations in soil labile P over days to weeks, particularly in soils at the wet end of the tropical forest precipitation spectrum where seasonal variability in rainfall and litterfall is less pronounced. In tropical forests where precipitation is rarely limiting, soil fertility and litter chemistry drive local-scale variation in decomposition and have the potential to influence the magnitude and timing of P response to environmental conditions (Hobbie and Vitousek, 2000; Wieder et al., 2009). For example, buffering of microbial immobilization in more fertile sites may lead to a more rapid release of P from decomposing material on soil wetting. It is unclear whether the effects of rainfall on P dynamics observed in drier tropical forests remain valid in the wettest regions of the tropics.

The size of the bioavailable P pool is strongly time dependent in P-deficient tropical soils as a result of rapid biological and geochemical P transformations (McKean and Warren, 1996; Olander and Vitousek, 2004, 2005; Vandecar et al., 2009). Rainfall can induce rapid changes in labile P through influences on P diffusion rates, geochemical reaction rates, leaching of P from the litter layer, decomposition rates, microbial biomass and activity, and plant uptake (Lodge et al., 1994; Chapin et al., 2002; Austin and Vitousek, 2000). Laboratory incubation studies of seasonal tropical and subtropical forest soils indicate that P responses to moisture are not always linear and that wetting can drive pulses in P availability on the scale of days to weeks (Campo et al., 1998; Grierson et al., 1998; DeLonge, 2007). Additionally, antecedent conditions and the level of wetting appear to modulate the magnitude and timing of P fluctuations, with heavy rain events leading to greater and more prolonged pulses in labile P (Campo et al., 1998; Grierson et al., 1998; DeLonge, 2007). Rain-induced pulses in P availability may be short-lived and the timing of sampling in relation to heavy rainfall events may have a significant impact on P estimates. Infrequent sampling in long-term nutrient cycling studies may not adequately capture transient environmentally driven fluctuations in labile P.

The main objectives of this study were: (i) to quantify in situ AEM P over various incubation lengths in two Oxisols of differing P content to improve our understanding of AEM dynamics in tropical soils; (ii) to evaluate the influence of environmental conditions (precipitation, temperature, and solar radiation) on soil labile P dynamics and determine time lags between environmental signals and P response; and (iii) to explore links between local vegetation characteristics (basal area, stem density, and species composition) and the minimum, maximum, mean, and range in AEM P.

MATERIALS AND METHODS

Study Site and Field Sampling

The study was conducted in mature tropical rain forest at La Selva Biological Station in the Caribbean lowlands of northern Costa Rica (10° 26′ N, 83° 59′ W; Organization for Tropical Studies). La Selva has a mean annual precipitation of 4300 mm (Organization for Tropical Studies, unpublished data (available online at http://www.ots.ac.cr/meteoro/default.php?pestacion=2 verified 26 Apr. 2011), with the driest period occurring between late January and April (McDade et al., 1994). Weekly rainfall ranges from 10 to 147 mm. Mean annual temperature is 25.8°C, with a much greater diurnal range in temperature (6–12°C) than the range in mean monthly temperature (<3°C; McDade et al., 1994). La Selva is characterized by deep, acidic, clay-rich soils that are volcanic in origin. They span a wide range of P fertility (Espeleta and Clark, 2007); soil P is sometimes in the deficient range and has the potential to limit plant growth (Denslow et al., 1987; Vitousek and Denslow, 1987) and litter production (Wood et al., 2009). The forest is predominantly evergreen (McDade et al., 1994) and is dominated by a N-fixing legume *Pentaclethra macroloba*, which accounts for as much as 36% of the basal area and 13% of stems (McDade et al., 1994; Lieberman et al., 1996; Clark and Clark, 2000).

Two sites on Oxisols of differing P content, approximately 1.2 km from one another (Fig. 1), were chosen for this study: CARBONO Plots A4 and L4 (total soil P: 1.18 and 0.46 Mg ha^{-1} (0–10 cm), respectively; Table 1; the CARBONO plot network is described in Espeleta and Clark, 2007). Concentrations of extractable P similar to those in the site with lower P content (Bray P 3 μg g^{-1}) have been associated with reduced plant growth in bioassays at La Selva (Vitousek and Denslow, 1987). In each 50 × 100 m (0.5 ha) plot, a 20 × 20 m subplot sampling area was established at each of four standardized locations within the plot (Fig. 1), to capture within-site variability. During the rainy season of 2005 (beginning on June 23rd), a set of five AEM replicates at approximately 5 cm spacing was placed at each of the four corners of a 0.5 m × 0.5 m square within each subplot (Fig. 1). One AEM from each of the four corners in each subplot was collected after 4, 8, 12, 20, and 24 d of incubation. After 4 d, a second series, consisting of three AEMs at each of the four corners of a 0.5-m^2 square, was installed within a few meters of the first series in each subplot. For the second series one AEM was collected from each of the four corners in each subplot after 4, 8, and 20 d of incubation. Two and four days following insertion of the second series another set of four AEMs was placed nearby in the same configuration and incubated for 12 and 14 d, respectively. This staggered deployment allowed us to collect the two series during the same visit to the field. Volumetric soil moisture was measured in the center of each plot by a Campbell CS615 (Campbell Scientific, Logan, UT) sensor (0–30 cm) calibrated for La Selva soils (Veldkamp and O'Brien, 2000) on three dates; before, during, and after the study.

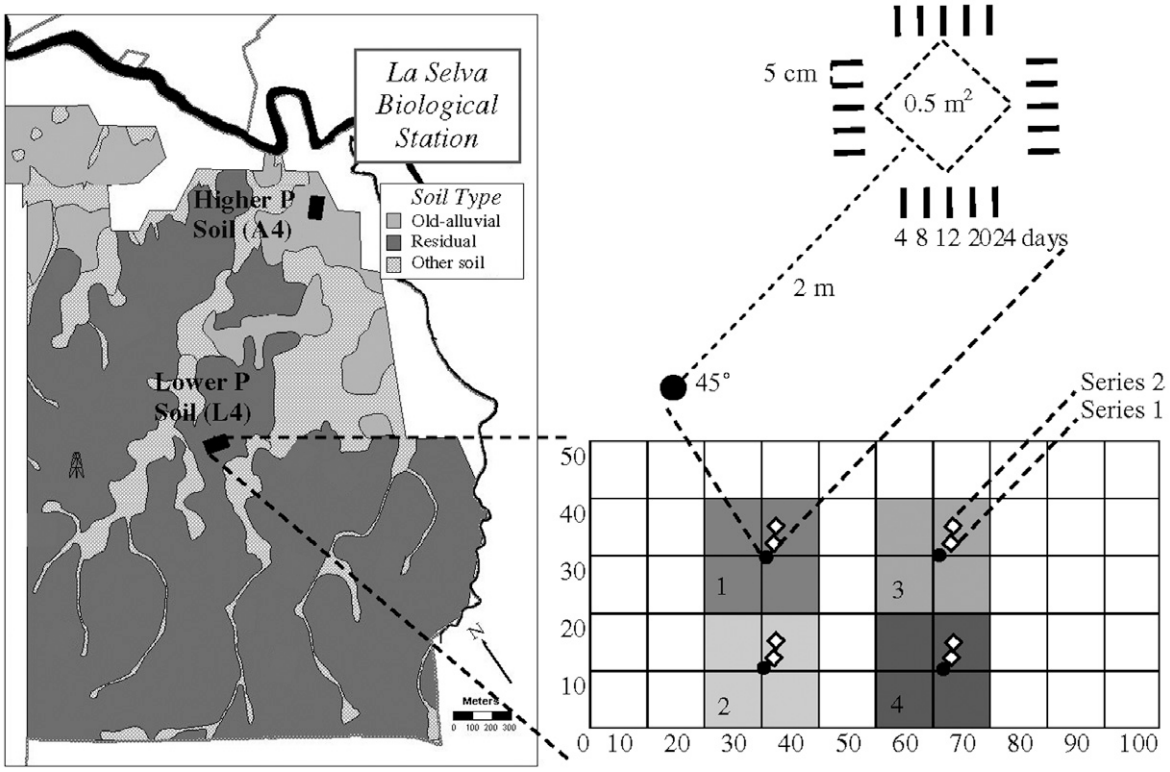

Fig. 1. Location of study plots and sampling design conducted in mature tropical forest at La Selva Biological Station in the Caribbean lowlands of northern Costa Rica. Samples were collected in a nested design with four 20 × 20 m subplots, numbered 1 through 4, at standardized locations within each plot. On 23 June 2005 a set of five anion exchange resin membranes (AEMs) at approximately 5-cm spacing were placed at the corners of a 0.5-m^2 sampling area near to and at a 45°angle from the center of each subplot. One AEM from each of the four corners of the sampling area was collected after 4, 8, 12, 20, and 24 d. A second set of three AEMs were placed in the same configuration around a second 0.5-m^2 sampling area and collected after 4, 8, and 20 d. Two and four days following insertion of the second series another set of four AEMs were placed in the same configuration and collected after 12 and 14 d.

Anion Exchange Resin Membrane Preparation and Chemical Analysis

The AEMs were cut into 2.5 by 5.0 cm strips; the equivalent of 1 g of dry resin (GE Infrastructure Sensing, Inc. Part Number A R204SZRA; formerly, Ionics part number 204-U-435). Each AEM contains approximately 1 g of dry resin and has the potential to accumulate 272 mg of P. Bright nylon fishing line was sewn onto each membrane so that it could be easily recovered in the field. The AEM strips were rinsed with deionized water (DIW) and presaturated with Cl^- using a 1 mol L^{-1} NaCl solution for at least 24 h before use. The Cl^- was chosen as the counterion rather than HCO_3^- to minimize effects on soil pH (Cooperband and Logan, 1994; Myers et al., 2005). Membranes were then rinsed with DIW and placed in widemouth bottles filled with DIW just before transportation to the field. Membranes were placed in the soil by making a vertical slit with a knife and then sliding the membrane in, so that it stood vertically just below the soil surface (0- to 5-cm depth). The soil was pressed down and inward around the membrane to ensure maximal contact on both sides. When membranes were recovered they were rinsed in the field with DIW and placed in individual sample bags filled with DIW and brought back to the laboratory before extraction. The AEMs were placed in 50-mL centrifuge tubes and shaken for 2 h with 20 mL of 0.5 mol L^{-1} HCl solution. Extractants were frozen in scintillation vials for later analysis. The P concentration of extracts was determined colorometrically using a molybdate blue methodology on an Alpkem Flow Solution IV Autoanalyzer (OI Analytical; College Station, TX).

Vegetation Structure and Composition

Basal area, stem density, and species composition were tabulated in September–October 2005 for all live stems with a diameter at breast height (DBH) greater than 10 cm within each 400 m^2 subplot (Table 2).

Statistical Analyses

All data were analyzed using SAS Systems for Windows V9.1 (SAS Institute, Inc., Cary, NC). The AEM P values greater than two standard deviations above the mean of all samples (n = 260) were considered

Table 1. Plot surface soil (0- to 10-cm depth) chemical and physical properties in mature tropical rain forest at La Selva Biological Station, Costa Rica (from Appendix L; Espeleta and Clark, 2007).

	Higher P soil (A4)	Lower P soil (L4)
pH in H_2O of dry soil	4.21	4.19
Bulk Density, g cm^{-3}	0.71	0.63
Effective cation exchange capacity, mmol(+) kg^{-1}	88.32	101.12
C stocks, Mg ha^{-1}	36.46	46.14
N stocks, Mg ha^{-1}	3.25	3.66
P stocks, Mg ha^{-1}	1.18	0.46
Bray P, μg g^{-1} (monthly average over 3 yr)	7.67	3.12
Fe, kg ha^{-1}	36.20	44.81
Al, kg ha^{-1}	461.75	455.72

Table 2. Subplot characteristics including vegetation structure and composition in mature tropical rain forest at La Selva Biological Station, Costa Rica.†

Characteristic	Higher P soil (A4)				Lower P soil (L4)			
	1	2	3	4	1	2	3	4
Stem density (no. trees per subplot)	10	14	16	20	25	20	28	22
Total basal area, m^2 ha^{-1}	20.1	27.4	24.8	34.4	14.3	9.4	39.8	30.5
Basal area of legumes, m^2 ha^{-1}	9.9	11.9	9.3	22.5	4.3	1.1	27.4	11.0
Basal area of palms, m^2 ha^{-1}	1.4	1.0	0.0	4.4	2.6	1.9	3.6	1.9
Dominant species (*% of total basal area*)								
Ampelocera macrocarpa Forero & A.H. Gentry Ulmaceae					8			
Balizia elegans (Ducke) Barneby & J.W. Grimes Mimosoideae							41	
Carapa nicaraguensis Audl. Meliaceae					11			
Dussia sp. Fabaceae				22				
Goethalsia meiantha (Donn. Sm.) Burret Tiliaceae	32		45					
Inga thibaudiana (DC.) Fabaceae					12			
Neea elegans P.H. Allen-vel aff. Nyctaginaceae					8			
Pentaclethra macroloba (Willd.) Kuntze Fabaceae	47	36	18	39	14		21	33
Protium panamense (Rose) I.M. Johnston Burseraceae						12		
Simarouba amara Aubl. Simaroubaceae		19						
Tapirira guianensis Aubl. Anacardiaceae								10
Trichilia septentrionalis C. DC. Meliaceae						12		
Virola koschnyi Warb. Myristicaceae						17		
Virola sebifera Aubl. Myristicaceae						14		
Xylopia sericophylla Standl. & L.O. Williams Annonaceae								16

† We measured all trees with a diameter at breast height of ≥10 cm. Each subplot had a total area of 400 m^2. The basal area from each subplot was scaled up to 1 ha to give units of m^2 ha^{-1}.

outliers (n = 10) and were not included in any analyses. Residuals of all analyses were checked for normality and homogeneity of variance. Data were log transformed when appropriate to meet the assumptions of analysis of variance (ANOVA). ANOVA was used to determine the effect of incubation length and soil total P content (site) on AEM P. Tukey–Kramer multiple comparison tests were used to determine significant differences between incubation lengths. When a significant effect of soil total P content (site) was found, a separate ANOVA was run for each site to determine the effect of subplot and incubation length on AEM P. To evaluate how P accumulation rate varied with incubation length, a t test was used to compare P estimates from one long incubation to the sum of P estimates from a series of shorter incubations covering the same time period (i.e., the sum of AEM P for 4-d incubations in Series 1 and 2 were compared with AEM P for the 8-d incubation in Series 1, see Fig. 2a; five such comparisons were made for each site). The coefficient of variation among replicates within a site ($11 \leq n \leq 16$; up to four replicates per subplot by four subplots) was calculated for each incubation length to compare spatial variability among sites. Some AEM replicates were not analyzed due to damage or drying in the field, however, each incubation length was represented by at least 11 AEMs and each subplot within an incubation was always represented by at least two AEMs.

Daily meteorological station data, including daily cumulative rainfall, mean temperature, and cumulative solar radiation were collected by the Organization for Tropical Studies (OTS) (available at http://www.ots.ac.cr/meteoro/default.php?pestacion=2, verified 26 Apr. 2011). Spatially averaged AEM P ($11 \leq n \leq 16$; up to four replicates per subplot × four subplots) was determined for each incubation length by site. This value was regressed against cumulative rainfall, mean temperature, and cumulative solar radiation during 1 up to 24 d before AEM removal from the soil (see Fig. 2a for removal dates). In other words, the climate conditions on the day before removal of AEMs from the soil were regressed against mean AEM P for each respective incubation length. Then climate conditions during the 2 d before AEM removal were summed or averaged and regressed against mean AEM P for each incubation length, and so on, up to 24 d before AEM removal. This resulted in 10 climate-AEM P pairs for each site (Series 1: 4,8,12, 20, and 24 d; Series 2: 4, 8, and 20 d, with an additional 12- and 14-d incubation during Series 2, Fig. 2a) that were used to test for differences in the tim-

ing, magnitude, and direction of P response to environmental signals as a function of total P content. In this case, the incubation length was disregarded as a factor, and the samples were treated simply as moments in time. Stepwise multiple regression was performed to determine if a combination of environmental drivers (rainfall, temperature, and solar radiation) could be used to predict AEM P during 1 up to 24 d before AEM removal from the soil.

Linear regression was used to explore the effect of subplot-level plant basal area, basal area of legumes, basal area of palms, and stem density on minimum, maximum, and average subplot AEM P (average of AEMs from all incubation lengths within a subplot), and range in AEM P over all incubation lengths. Regressions were then run again with average subplot AEM P normalized by site mean AEM P (a *z*-score) so the two plots could be combined in one analysis.

RESULTS

Soil Total Phosphorus Fertility and Incubation Length Effects

Over the 24 d, mean AEM P among all incubation lengths ranged from 0.26 to 1.38 μg membrane^{-1} in the site with higher P content; on average 170% higher than the site with lower P content (0.11–0.77 μg membrane^{-1}, Fig. 2d). The range in AEM P values across all incubation periods, once outliers were removed, was 0 to 3.87 μg membrane^{-1} in the more P-deficient site and 0 to 4.37 μg membrane^{-1} in the site with higher P content. The AEM P varied significantly by incubation length ($F = 10.17$, $p < 0.0001$) and by total P content (site) ($F = 75.97$, $p < 0.0001$). When sites were tested independently for subplot and incubation length effects, incubation length was a significant driver in both sites (A4: $F = 6.36$, $p < 0.0001$, L4: $F = 5.29$, $p = 0.0002$), but subplot was not. In the site with higher P content (A4) AEM P increased consistently with incubation length, while in the site with lower P content AEM P was lowest for 8-d incubations, peaked at 14-d incubations and then declined with incubation length. The coefficient of variation (CV) between replicates within an incubation period ($n = 16$) was on average 110% higher in the site with lower P content. We found that short incubations, particularly 4-d incubations, provided labile P estimates that were quite variable (potentially due to soil disturbance on insertion), while longer AEM incubations were associated with lower coefficients of variation. Longer incubations yielded significantly lower estimates of P availability than a series of shorter deployments covering the same time period in the site with higher P content ($t = 2.66$, $p = .0281$, df = 4). However, in the more P-deficient site there was no consistent pattern between P estimated from one long incubation and P estimated from the sum of a series of shorter incubations.

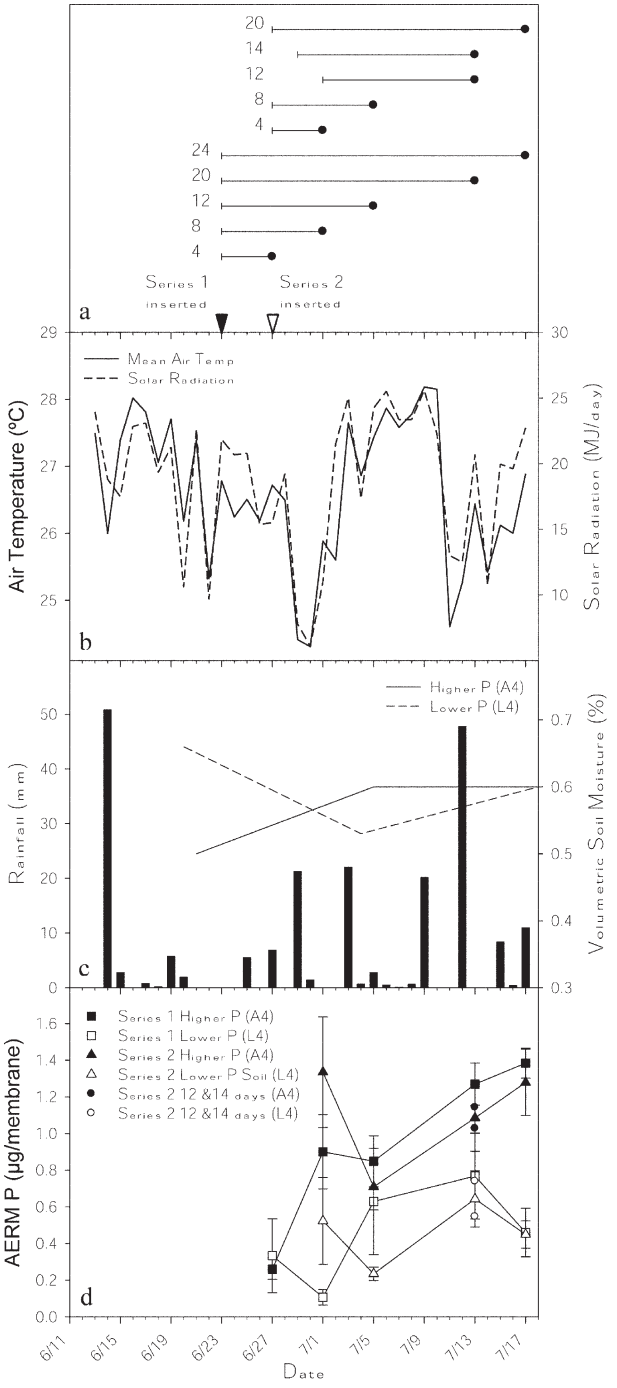

Fig. 2. (a) Incubation lengths for Series 1 and 2 with solid circles representing removal dates. Environmental conditions before and during the 24-d study: (b) temperature and solar radiation, and (c) rainfall and volumetric soil moisture. (d) Spatially averaged Anion exchange resin membrane-P (AEM-P) values for each incubation length in Series 1and 2 for both sites with error bars representing ±1 standard error. The 12- and 14-d AEM-P values for Series 2 were averaged and plotted on 13 July 2005 when both were extracted (a); actual 12- and 14-d values were also plotted as solid circles for the soil with higher P content and open circles for the soil with lower P content (14-d values are higher than 12-d values for both sites).

Environmental Controls on Anion Exchange Resin Membrane Phosphorus

In the site with higher P content, AEM P was positively related to cumulative rainfall during the 6 d before AEM removal and up to 13 d prior (though not significant for 11 d prior), as well as 18 and 19 d prior (Fig. 3a). This relationship was strongest for cumulative rainfall during the 6 d before AEM removal ($r^2 = 0.54$, $F = 9.52$, $p = 0.0150$, Fig. 4a). In the site with lower P content AEM P was positively related to cumulative rainfall during the 2 d and up to 5 d before AEM removal (Fig. 3a). This

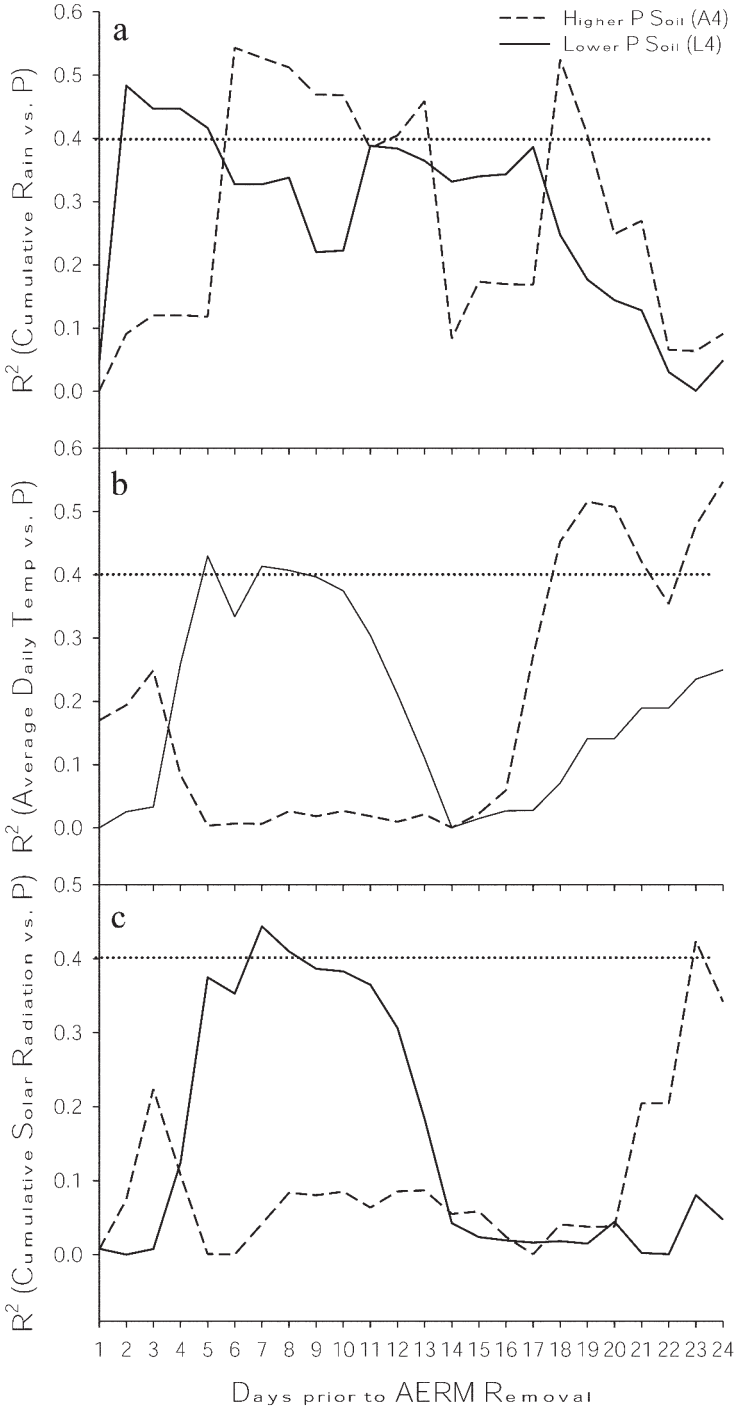

Fig. 3. The r^2 values from regressions of spatially averaged AEM P for each incubation length as a function of: (a) cumulative rainfall, (b) mean temperature, and (c) cumulative solar radiation, during 1 up to 24 d before AEM removal from the soil in both study sites. Dotted lines mark the cutoff for r^2 values that are significant at a p value of <0.05.

relationship was strongest for rainfall during the 2 d before AEM removal (r^2 = 0.48, F = 7.49, p = 0.0256, Fig. 4b).

In the site with higher P content, AEM P was negatively related to mean temperature during the 18 d and up to 24 d before AEM removal (though not significant for 22 d prior, Fig. 3b), with the strongest relationship for 24 d prior (r^2 = 0.55, F = 9.66, p = 0.0145, Fig. 5a). The AEM P was negatively related to cumulative solar radiation during the 23 d before removal (r^2 = 0.42, F = 5.86, p = 0.0417, Fig. 3c). The AEM P in the more P-deficient site was positively related to mean temperature during the 5 to 8 d before AEM removal (though not significant for 6 d prior, Fig. 3b), with the strongest relationship during the 5 d prior (r^2 = 0.43, F = 6.03, p = 0.0396, Fig. 5b). The AEM P was positively related to cumulative solar radiation during the 7 to 8 d before AEM removal with the strongest relationship during the 8 d prior (r^2 = 0.44, F = 6.38, p = 0.0355, Fig. 3c). Mean temperature and cumulative solar radiation were correlated with one another during the study period of June 23 through July 17 (r^2 = 0.75, F = 67.48, p < 0.0001, Fig. 2b).

In a stepwise multiple regression, 83% of temporal variability in mean AEM P for the site with higher P content was explained by a combination of cumulative rainfall (positively related) and cumulative solar radiation (negatively related) during the 19 d before AEM removal (r^2 = 0.83, F = 16.73, p = 0.0022). Considering those factors during 18 rather than 19 d prior lowered the variance explained to 77% (r^2 = 0.77, F = 11.78, p = 0.0058). In the more P-deficient site no combination of factors explained more of the variation than the single factors (cumulative rainfall, mean temperature, and cumulative solar radiation) in the univariate regressions.

Vegetation Structure and Composition Effects

Subplot-level plant basal area and basal area of legumes, which were correlated with one another (r^2 = 0.88, F = 43.10, p = 0.0006), were positively related to average AEM P within each site, although due to the small sample size (four subplots) the relationship was only significant for basal area of legumes in the site with lower P content (r^2 = 0.97, F = 61.01, p = 0.0160). When subplot average AEM P values were normalized for site mean AEM P (z-scores), subplot level total basal area explained 74% (r^2 = 0.74, F = 17.13, p = 0.0061, Fig. 6a) and basal area of legumes explained 89% (r^2 = 0.89, F = 46.48, p = 0.0005, Fig. 6b) of the variation in normalized AEM P across sites. Stem density and basal area of palms were not significantly related to average AEM P or normalized AEM P. Minimum and maximum AEM P, and range in AEM P over all incubation periods were not related to subplot-level total basal area, basal area of legumes, basal area of palms or stem density.

DISCUSSION

The range in spatially averaged AEM P over our 24-d study (0.11–1.38 mg kg^{-1} resin) was comparable with the range reported for monthly 10-d in situ AEM incubations in a P-poor Amazonian agroforest Ultisol over a 14-mo period (0.014–1.62 mg kg^{-1} resin; McGrath et al., 2000). On the whole, our results demonstrate that labile P in tropical soils is sensitive to environmental conditions and is quite variable on a

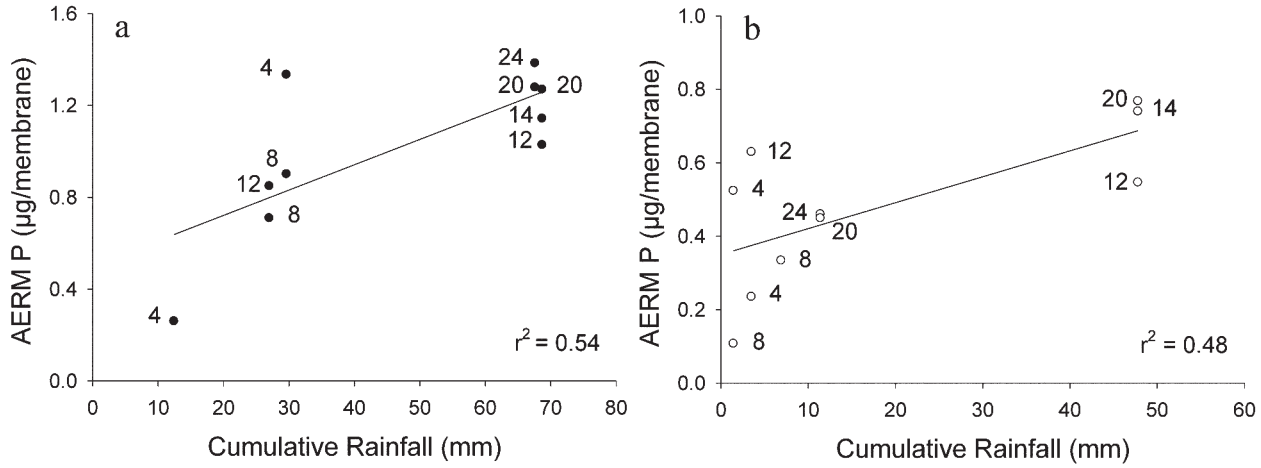

Fig. 4. Spatially averaged AEM P for each incubation length as a function of cumulative rainfall during: (a) the 6 d before AEM removal in the site with higher P content and (b) the 2 d before AEM removal in the site with lower P content. Number labels indicate incubation lengths.

submonthly timescale. This work has implications for the methodological design of long-term P cycling studies and suggests that infrequent soil P measurements may not adequately capture environmentally driven variability in labile P.

Our study design of deploying two overlapping series of incubations in soils of contrasting P fertility allowed us to address a number of questions about the effects of incubation length on AEM P estimates in tropical forest soils. Congruent with previous investigations of AEM P dynamics under field conditions in P-deficient soils, our overlapping series of incubations revealed nonlinear AEM accumulation (Drohan et al., 2005; Meason and Idol, 2008). Although AEMs in the site with higher P content appeared to accumulate ions throughout the 24-d study, the rate of P accumulation declined such that a series of short incubations always yielded higher P estimates than one long incubation covering the same time period. In contrast, AEMs in the more P-deficient site did not continue to accumulate P throughout the study, but peaked at 14 d and subsequently declined, which seems to indicate AEMs were acting as dynamic exchangers. Our findings support the interpretation of in situ AEM P as an equilibrium estimate of labile P that integrates soil sorption capacity and biological demand, rather than an estimate of gross P flux through the available pool during the incubation.

To choose an appropriate AEM incubation length for P cycling studies in tropical soils, it is important to know when AEMs transition from being infinite sinks to dynamic exchangers of P. There is no standard length for AEM incubations and those reported in the literature range from hours to longer than 6 mo. The time needed for AEMs to equilibrate with soil labile nutrient pools appears to be site-specific, ranging from 2 wk to possibly longer than 24 d in our soils. Given that incubation length can affect the detection and magnitude of treatment effects (Meason and Idol, 2008), optimum periods of burial should be chosen carefully based on preliminary testing of the soils under study. Despite site-specific differences in incubation length effects, AEMs were able to detect fine-scale temporal and spatial variation in in situ P availability associated with environmental conditions and vegetation characteristics.

Multiple regression analysis revealed that up to 83% of the temporal variation in labile P could be explained by environmental conditions over days to weeks. However, the timing and in some cases the direction of labile P responses to environmental conditions differed as a function of total P status. Despite

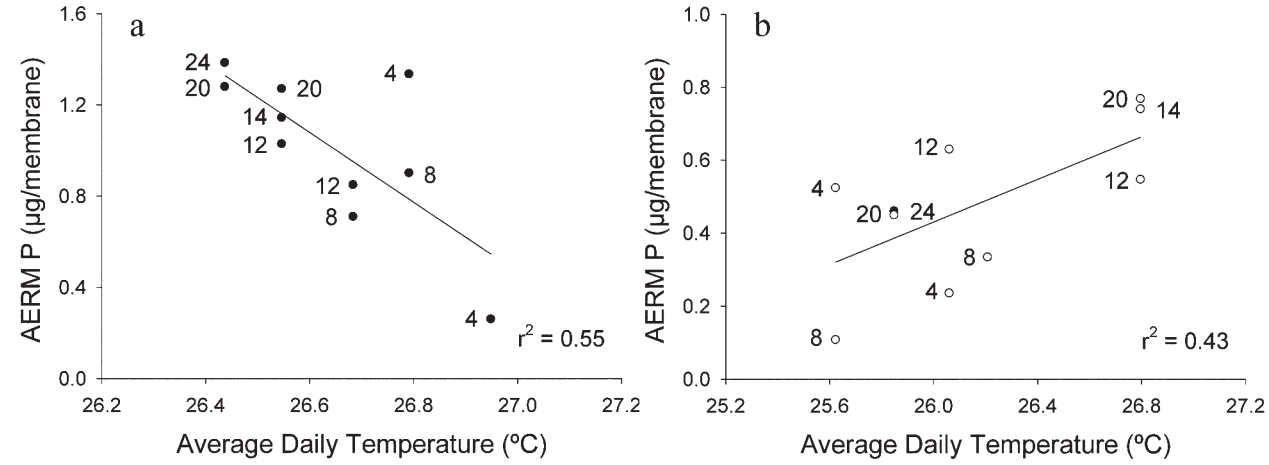

Fig. 5. Spatially averaged AEM P for each incubation length as a function of mean temperature during (a) the 24 d before AEM removal in the site with higher P content and (b) the 5 d before AEM removal in the site with lower P content. Number labels indicate incubation lengths.

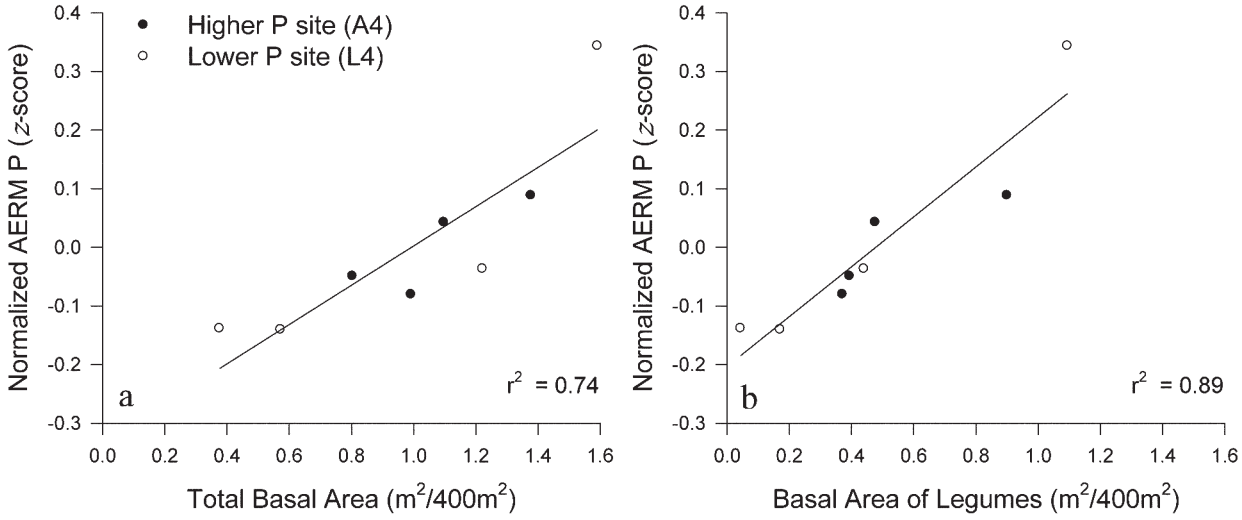

Fig. 6. Subplot level: (a) total plant basal area and (b) basal area of legumes for Plot A4 (solid) and L4 (open) versus normalized mean subplot AEM P across all incubation lengths.

consistently high soil moisture (50–66%) throughout the study, the factor that best explained variability in AEM P was rainfall, which was positively associated with labile P in both sites. Although, soil saturation can lead to anoxic conditions that slow decomposition (Schuur and Matson, 2001), recent evidence suggests that leaching of dissolved organic matter from litter and potentially nutrient mineralization may increase with rainfall up to very high levels of precipitation (Cleveland et al., 2006; Wieder et al., 2009). Although we can only speculate about the mechanisms driving the patterns we observed in AEM P, it is possible that P solubilization associated with iron reduction in anoxic microsites may have contributed to greater P availability with increasing rainfall (Miller et al., 2001; Wright et al., 2001; Peretyazhko and Sposito, 2005; Chacon et al., 2006). Our results demonstrate that rainfall patterns in wet tropical forests generate variability in labile P on the timescale of days to weeks, however, further research is needed to determine how the mechanisms driving this relationship differ from those in drier tropical soils.

Across a range in rainfall conditions (five different removal dates, see Fig. 2a), we found that the less fertile soil exhibited a more immediate response to rainfall, with the strongest coupling between rainfall and AEM P in the range of 2 to 5 d before AEM removal from the soil as opposed to 6 to 13 and 18 to 19 d in the site with higher P content. Given that our sites experienced similar environmental conditions during the study, differences in the timing of P responses to rainfall are likely the result of biological controls. The more rapid response in the P-poor soil is at odds with our hypothesis that microbial immobilization may lead to a delayed response to environmental drivers in less fertile soils. An alternative explanation is that greater microbial and plant production of phosphatase in the P-poor soil may lead to more rapid release of P from soil organic material as soil moisture increases. An influence of soil moisture on the production and the activity of phosphatase enzymes has been reported in a number of ecosystems, however, these results are quite variable and more research is needed to identify any potential phosphotase effect (Chen et al., 2003; Criquet et al., 2004; Yavitt et al., 2004; Sowerby et al., 2005).

The size and intensity of rainfall events has a strong influence on subsequent microbial contributions to labile P (Yang and Insam, 1991; Lodge et al., 1994; Campo et al., 1998). Campo et al. (1998), using a lab incubation of dry tropical forest soils collected during the wet season, found that microbial immobilization of P was stimulated by a 30-mm simulated rainfall event but not a 10-mm event. The one very large rain event (47.8 mm on 12 July 2005 that occurred during our study marked a divergence in P patterns in our two sites. This event was followed by a temporary increase in AEM P (captured in both the Series 1- to 20-d incubation and the Series 2- to 12- and 14-d incubations) in both sites, followed by a decline in labile P (captured in both the Series 1- to 24-d incubation and the Series 2- to 20-d incubation) in the more P-poor site. No corresponding decrease in AEM P was observed in the site with higher P content. Given that the importance of biological controls on labile P dynamics increases as P availability declines (McGill and Cole, 1981; Walbridge, 1991; Dakora and Phillips, 2002; Olander and Vitousek, 2004, 2005; Barroso and Nahas, 2005) greater biological demand in the more P deficient site may explain this observation.

Temperature, one of the primary regulators of microbial activity, is known to influence many processes relating to nutrient availability and plant uptake. Under field conditions and in lab incubation studies positive effects of temperature on labile P have been observed, although they tend to be less important than moisture effects (Yang et al., 1991; McKean and Warren, 1996; Vandecar et al., 2009). We found that labile P responded positively to temperature (and solar radiation) in the more P-deficient site, during the 5 to 8 d before AEM removal. However, labile P declined with temperature (and solar radiation) in the site with higher P content, during the 18 to 24 d before AEM removal. Given that temperature and solar radiation covaried during the study, our ability to distinguish their relative influences on P patterns is limited. Greater microbial controls over P dynamics

in the more P-deficient site is consistent with the positive and more immediate response to temperature, on AEM P patterns observed there.

Vegetation structure at the subplot-scale appeared to play a role in driving spatial heterogeneity in mean soil labile P, such that higher basal area was associated with higher mean P availability in both sites. These results should be viewed with caution given the small sample size (eight subplots), however, this relationship has been reported previously, on a similar spatial scale (tens of meters), at a different site in this forest (Vandecar et al., 2009). Evidence of rhizosphere-enhanced mineralization of P from soil organic matter has been detected by AEMs in greenhouse soil incubations (Johnson et al., 2007). Vegetation-driven local P enrichment of surface soils may also be attributed to uptake of P from deeper soil layers, that is subsequently deposited on the forest floor as litter. Litterfall inputs, which correlate well with within-stand basal area at La Selva, (Lawrence unpublished data,200–2002), represent one of the primary sources of plant available P. Legume species common in tropical forests may also contribute to local P enrichment by releasing more phosphatase into the soil than non-legume species to support N-fixation (Houlton et al., 2008). Total basal area and basal area of legumes (which were correlated with one another) explained 74 and 89% of the variation in mean AEM P among subplots, respectively.

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