Biogeochemistry (2016) 127:35–43
DOI 10.1007/s10533-015-0150-z

Short-term variability in labile soil phosphorus is positively related to soil moisture in a humid tropical forest in Puerto Rico

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Received: 7 January 2014 / Accepted: 13 October 2015 / Published online: 16 December 2015

Abstract Primary productivity in tropical forests is often considered limited by phosphorus (P) availability. Microbial activity is a key regulator of available P through organic matter decomposition (supply) as well as microbial immobilization (depletion). Environmental conditions, such as soil moisture and temperature can fluctuate significantly on hourly to daily timescales in tropical forested ecosystems. Given the ability of microbes to respond rapidly to changing environmental conditions we would expect concomitant changes in the available soil P pool. Despite the potential for soil P availability to vary on short timescales, research that investigates hourly to daily changes in the available soil P pool in tropical forests is extremely rare. We quantified diurnal fluctuations in labile soil P and the importance of biotic and abiotic factors in driving these patterns in a wet tropical forest in Puerto Rico. Hourly measurements of Bray-extractable P were made from sunrise to sunset on five separate days along with measurements of soil temperature, moisture, pH, soil respiration, and solar radiation. While we found no significant diurnal variation in labile P, it did, however, vary significantly across the five sample days (2.8–3.8 µg/g). The day-to-day variation in labile P was positively related to soil moisture ($R^2 = 0.42$, $p = 0.009$). These findings illustrate the potential for rapid change in the available P pool in response to variable soil moisture status as well as the importance of considering soil moisture conditions when estimating P availability in the humid tropics.

Keywords Tropical forest · Luquillo experimental forest · Phosphorus · Bray-1 P · Diurnal · La Selva Biological Station

Responsible Editor: Jonathan Sanderman.

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Introduction

Highly weathered Ultisols and Oxisols are the most common soil types in lowland tropical forests. These soils are typically deficient in rock-derived nutrients, such as phosphorus (P) (Walker and Syers 1976; Yang and Post 2011), and as such, tropical forested ecosystems are often considered to be primarily limited by P (Vitousek 1984). There is ample evidence to support this supposition, including but not limited to effects on nutrient resorption (Mayor et al. 2014; Townsend et al. 2007; Tully et al. 2013), soil respiration (Cleveland and Townsend 2006; Wood and Silver 2012) and litter production (Cleveland et al. 2011; Wood et al. 2009). As in any ecosystem, there is potential for multi-element limitation in tropical forested ecosystems (Townsend et al. 2011). Nevertheless, understanding the factors that control P availability in tropical forests could provide invaluable insight into how future change might affect these important ecosystems.

Studies have shown that large seasonal fluctuations in rainfall, typical of tropical forested ecosystems, can drive changes in biologically available P such that concentrations in the soil are highest just after the onset of the wet season (Campo et al. 1998; Lodge et al. 1994; McGrath et al. 2000; Singh et al. 1989; Wood and Lawrence 2008). However, tropical forests also experience punctuated rainfall events that occur on much shorter, daily time-scales. These punctuated rainfall events can lead to abrupt spikes in soil moisture that have the potential to stimulate changes in soil chemistry (e.g., redox potential, pH, desorption of nutrients from minerals; Chacon et al. 2006; Hall et al. 2013; Kieft et al. 1987; Liptzin et al. 2011; Vandecar et al. 2011; Wood et al. 2013) as well as microbial and plant activity (Cleveland et al. 2004; Kieft et al. 1987; Singh et al. 1989; Tiessen et al. 1994). Increased soil moisture content could additionally stimulate an increase in decomposition rates (Birch 1958; Cusack et al. 2009; Liang et al. 2003), and P is replenished in large part through decomposition of organic matter by microbes (Singh et al. 1989; Tiessen et al. 1994). Thus, increased soil moisture can result in P bound to organic matter being released and made part of the available P pool. Ultimately, soil moisture's effect on these factors may cause rapid fluctuations of the pool of available P over hourly to daily timescales.

In most tropical forest ecosystems variability in temperature is much greater on diurnal time-scales than it is on longer, seasonal time-scales. For example, temperature can change as much as 13 °C diurnally, compared with just a 4 °C change in mean temperature throughout the year (Garcia-Martino et al. 1996). Microbial activity generally increases with increasing soil temperature (Cusack et al. 2010; Davidson and Janssens 2006; Holland et al. 2000; Jonasson et al. 1999; Liang et al. 2003; Meentemeyer 1978; Wood et al. 2012), adding to the pool of labile P as microbes begin turning over nutrients as the sun rises and the temperature warms. Increases in temperature throughout the day can also influence microbial decomposition rates, thereby releasing P bound in organic matter and increasing the amount of available P in the soil. While an increase in microbial mineralization rates increases the amount of available P, microbes also allocate resources to growth, which would instead immobilize labile P, thereby reducing its availability in the soil as microbial activity increases (Cleveland et al. 2004; Lodge et al. 1994).

As with temperature, light availability also changes throughout the day. Solar radiation is a key driver of plant photosynthesis, which has been shown to stimulate root activity (Tang et al. 2005; Yuste et al. 2010; see also Vandecar et al. 2009). This increase in root activity could lead to additional drawdown of labile soil P in the soil during periods of high demand and high root uptake. Plant activity usually peaks around midday, which could lead to a stronger drawdown of labile soil P during this time (Vandecar et al. 2009). Given the potential influence of root density on labile soil P uptake, the potential for a strong diurnal pattern in the size of the labile soil P pool is likely to be greater in sites with higher soil respiration rates and basal area (Pregitzer et al. 1998; Vandecar et al. 2011; Vandecar et al. 2009).

Soil carbon dioxide (CO_2) efflux is the product of both root and heterotrophic bulk soil respiration (Medina and Zelwar 1972; Silver et al. 2005) and can be used to demonstrate root and microbial activity. There is evidence of both diurnal and seasonal variation in soil CO_2 efflux in tropical forested ecosystems, and this variability has been correlated with soil temperature (Schwendenmann and Veldkamp 2006; Schwendenmann et al. 2003; Sotta et al. 2004, 2006; Vandecar et al. 2009; Wood et al. 2013; Wood and Silver 2012), soil moisture (Chambers et al. 2004; Schwendenmann and Veldkamp 2006; Schwendenmann et al. 2003; Sotta et al. 2007; Wood and Silver 2012), and soil P availability (Vandecar et al. 2009; Wood and Silver 2012). Higher soil CO_2 efflux reflects enhanced rates of heterotrophic activity, thus potentially increasing the amount of P in the soil. At the same time, high CO_2 efflux could indicate more root respiration and thus an increase in the uptake of labile soil P. As such, evaluating the short-term variability in soil CO_2 efflux could provide insight into the overall activity of soil roots and microbes, and depending on the time-scale of variability, the dominant processes controlling soil P availability.

Research that investigates hourly to daily changes in available soil P in tropical forests is extremely rare, and we know of only one study to date that has evaluated changes in the labile P pool on this time-scale (Vandecar et al. 2009). Given the potential for P to limit key processes in tropical forested ecosystems (e.g., plant biomass production and microbial metabolism), research that evaluates the time-scale over which this nutrient varies is valuable for predicting future responses (Reed et al. 2015). Here, we examine variability in the pool of labile soil P both within a single day and among days in a humid tropical forest in Puerto Rico and assess whether the results found by Vandecar et al. (2009) hold for other tropical forest sites. We further investigated the potential for environmental controls (e.g. temperature, solar radiation, soil moisture) on available soil P and for root and microbial responses using CO_2 efflux as an index of their activity (Vandecar et al. 2009) and tree basal area as a proxy for indirect effects of plant organic matter inputs (Yanai et al. 2012).

Methods

Study site

The research was conducted in northeast Puerto Rico in the Bisley Experimental Watersheds, which are part of Luquillo Long-term Ecological Research (18°18′N, 65°50′W; Wood and Silver 2012). The site is classified as subtropical wet forest (Holdridge 1967), receives on average 3500 mm of rainfall per year, and has a mean annual temperature of 23 °C (Garcia-Martino et al. 1996). While precipitation is highly variable throughout the year, there is no significant dry season and mean monthly temperature varies just 4 °C throughout the year (Heartsill-Scalley et al. 2007). The soils are classified as Ultisols and have a high percentage of clay (Scatena 1989; Table 1). We worked in a riparian valley that is dominated by *Prestoea Montana* R. Graham Nichols (Wood and Silver 2012), a palm species prevalent throughout the watershed (Scatena 1989; Table 1). Palm forest occurs discontinuously across the entire elevational range of the Luquillo Mountains. While it is most abundant at higher elevations, it is also important along drainages and streams to low elevations (Foster et al. 1999), and has been found to have higher available soil P than comparable dicotyledonous forest (Wood and Silver 2012).

Experimental design

We worked in three 1.54 m^2 plots that were established a minimum distance of 4 m apart (plots 2, 6 and 10 from Wood et al. 2013; Wood and Silver 2012). We used time-domain reflectometry (TDR, Campbell Scientific Model CS616) to estimate hourly soil moisture in all plots (0–30 cm), and measured hourly soil temperature (10 cm; Campbell Scientific, Model 108L) in one plot. Automated soil respiration chambers (Li-Cor LI-8100/8150 Multiplexer; Li-Cor Biosciences, Lincoln, NE, USA) were installed in all three

Table 1 Plant and soil characteristics of the field site

Variable	Plot 2	Plot 6	Plot 10
Dominant species (% Basal Area)[a]	*Prestoea montana* (33 %) *Cecropia schreberiana* (18 %) *Dacryodes excelsa* (15 %)	*Prestoea montana* (88 %) *Cyathen arborea* (5 %) *Cecropia schreberiana* (4 %)	*Andira inermis* (36 %) *Cecropia schreberiana* (32 %) *Prestoea montana* (13 %)
Total Basal area (m^2)[a]	2.7	7.5	4.4
Volumetric soil moisture (m^3/m^3)[b]	0.42	0.44	0.32
Bray P (μg P/g)[b]	3.5	3.6	2.8
Inorganic NO3$^-$ (μg N/g)[a]	1.87	1.18	1.26
Inorganic NH_4^+ (μg N/g)[a]	1.7	1.21	3.62

[a] From Wood and Silver (2012); soils are 0–10 cm, analyzed 29 July 2008; Basal area = All stems ≥ 10 cm DBH in 5 m circular radius from center of each plot

[b] This study; soils are 0–10 cm, n = 9

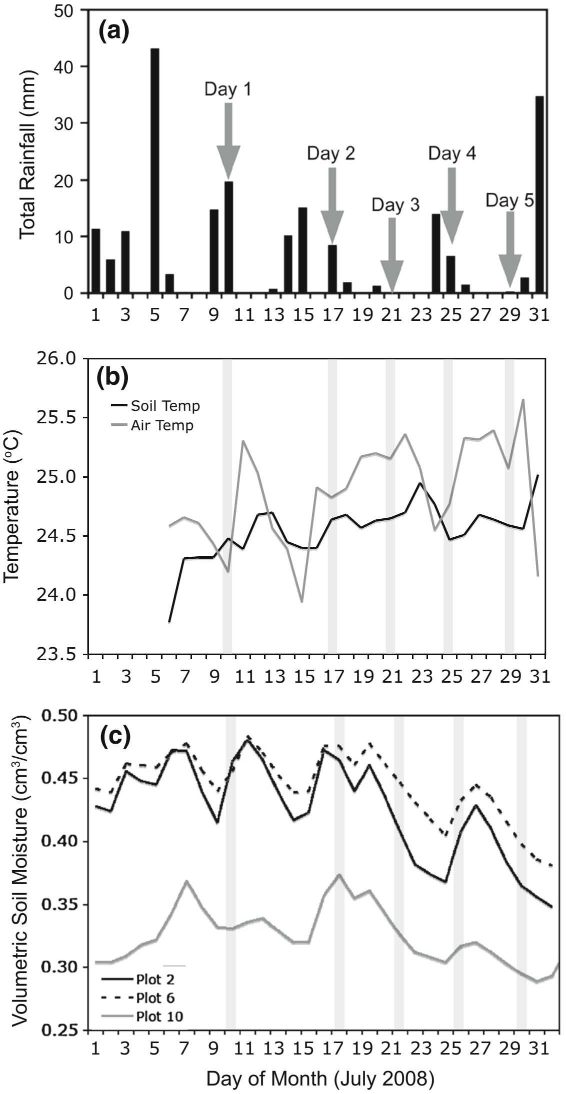

Fig. 1 **a** Total precipitation per day, **b** mean daily soil and air temperature and **c** mean daily volumetric soil moisture values for each of the three study plots for the month of July 2008. *Arrows* and *shaded areas* indicate when sampling occurred

plots to measure hourly changes in soil CO_2 efflux. For more details on the experimental design see Wood et al. (2013).

In July 2008 we collected soils on 5 days (July 10, 17, 21, 25, 29–30) that included a range of precipitation events (Fig. 1). This period is just after the onset of the wetter, hurricane season at Luquillo. On the first three days (July 10, 17, 21) we collected soils from 6 a.m. to 6 p.m. at 2 h intervals. On the fourth day (July 25) we collected soils hourly from 5 a.m. to 7 p.m. We increased the frequency and duration of sampling on the fourth day due to an increase in sampling efficiency, which made this possible, and because we were interested in whether the hours prior to sunrise and after sunset were important. On the fifth day (July 29–30) we collected soil cores hourly from 5 a.m. to 7 p.m. and then bi-hourly from 9 p.m. to 3 a.m. as part of a 24-h study. Since two people alone were responsible for all soil collections, we changed from hourly to bi-hourly sampling over the 24-h period so that one person would be able to sleep. During each sample period we collected three soil cores (2.5 cm dia.) to 10 cm from each plot, for a total of nine cores per sample period. To avoid over-sampling, we shifted collection locations by 0.5 m on each collection day. All stems within a 4 m radius of the center of each plot with a DBH >5 cm were measured and the species identified (Table 1). Ambient temperature, precipitation, solar radiation and relative humidity were recorded at hourly intervals at a meteorological tower within ~500 m of the work site.

Chemical analyses

Due to the frequency of sampling, we set up a field laboratory and conducted all extractions in the field immediately after soil samples were collected. We analyzed labile soil P using a Bray-1 extraction (Bray and Kurtz 1945). We weighed 5 g of soil from each soil core into sterile 50 mL centrifuge tubes containing 25 mL of a 0.03 N ammonium fluoride (NH_4F) and 0.025 N hydrochloric acid (HCL) solution. These samples were shaken for 1 min and allowed to settle (Bray and Kurtz 1945). After settling, the top layer was pipetted into sterile 23 mL scintillation vials and frozen within 24 h of extraction. At the same time, we weighed an additional 5 g of soil from each core on individual, pre-weighed aluminum foil squares. These squares were then folded into packets and oven-dried at 105 °C for 24 h to determine gravimetric soil moisture. Frozen Bray-1 extracts were shipped to the University of Virginia where they were analyzed for labile soil P colorimetrically using a molybdate blue methodology on an Alpkem flow solution IV Autoanalyzer (OI Analytical; College Station, Texas, USA) in accordance with the US EPA method for P. All data are reported on a dry mass basis.

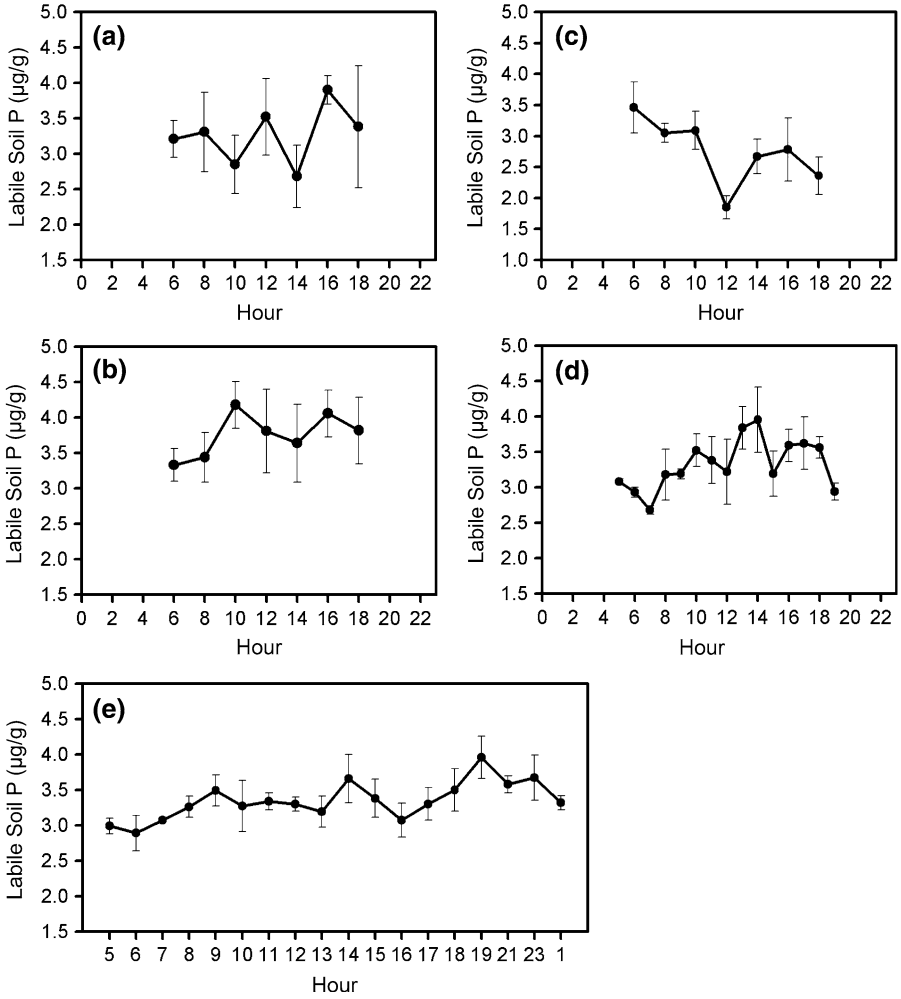

Fig. 2 Mean hourly variation in labile soil P (±S.E.) on **a** Day 1, **b** Day 2, **c** Day 3, **d** Day 4, and **e** Day 5

Statistical analyses

We determined whether variables differed significantly within and among days and among the three plots by repeated measure analysis of variance (ANOVA) in SAS Systems for Windows V9.1 (proc Mixed, SAS Institute, Inc.). We performed stepwise multiple regressions to model labile P based on a combination of the measured environmental factors also using SAS Systems for Windows V9.1 (SAS Institute, Inc.). Once we knew which variables were important, we used regression analyses to determine the shape of the relationship between changes in labile soil P (mean of three replicates per plot) and mean soil characteristics (e.g., soil moisture and temperature). When significant diurnal variation was observed, regressions were performed using mean hourly values. All other regressions were performed using mean daily values. Regressions were performed using SigmaPlot 10 (SigmaPlot for Windows, v. 7.101, 2001, SPSS Inc.).

Results

Temporal and spatial variation in labile P

Labile P did not vary significantly on an hourly timescale (F = 1.29, p = 0.28, df = 62) on four of the five sample days, with a mean within day coefficient of variation of 13 % (Fig. 2). The only day on which labile P varied significantly was over the 24-h sample period, with values ranging from 2.9 to 4.3 µg/g (F = 2.05, p = 0.032, df = 18). On this day, values increased steadily throughout the day, peaking at

7 p.m. (Fig. 2e). Labile soil P varied significantly across the five sample days (F = 16.54, $p < 0.0001$, df = 315), ranging from 2.8 to 3.8 µg/g, and among the three plots (F = 84.65, $p < 0.0001$, df = 165). One plot demonstrated significantly lower labile soil P than the other two plots (2.8 vs 3.6 µg/g). It is of note that *Andira inermis* was the dominant tree near the low P plot, while *P. montana*, which has been found to have higher foliar P concentrations (Scatena 1989) and higher available soil P concentrations (Wood and Silver 2012), was the dominant species near the remaining two plots.

Controls on labile soil P

Labile soil P did not vary on a diurnal timescale on Days 1–4, thus we did not perform regression analysis with environmental variables for these days. On Day 5, which did demonstrate significant diurnal variation, we found a significant negative relationship between volumetric soil moisture and Bray P (i.e., the 24-h period; $R^2 = 0.34$, $p = 0.035$). We found no significant relationship between Bray P and soil CO_2 efflux, soil temperature or light availability over the 24-h period. Interestingly, when we exclude Day 5 from an analysis evaluating the relationship between mean hourly volumetric soil moisture and Bray P across days we find a significant positive relationship between volumetric soil moisture and labile soil P (Fig. 3; $R^2 = 0.28$, $p = 0.001$). Furthermore, when we evaluate mean daily volumetric soil moisture and Bray P (average of hourly values for each plot for each of the five sample days), we also find a positive relationship between labile soil P and volumetric soil moisture (Fig. 4; $R^2 = 0.42, p = 0.009$). As with hourly variation in Bray P, there was no significant relationship between Bray P and soil temperature, light and soil CO_2 efflux when considering variation across days. This finding is supported by results from a stepwise multiple regression that included all 5 days, which eliminated all of the variables from the model, at an α-level of 0.05, with the exception of volumetric soil moisture. In this model, volumetric soil moisture explained 30 % of the variability in labile soil P ($r^2 = 0.30, p < 0.0001$).

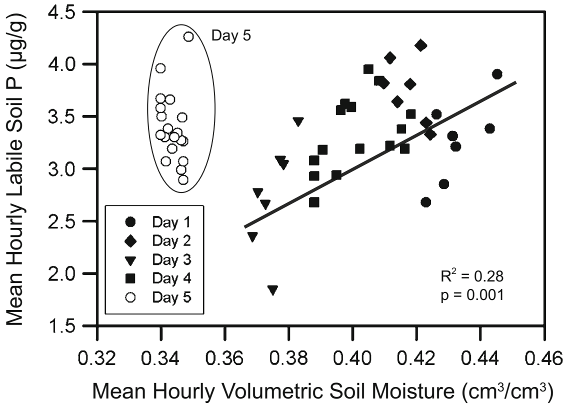

Fig. 3 Regression between hourly labile soil P and volumetric soil moisture when Day 5 is not included in the regression. Symbols represent different sampling days

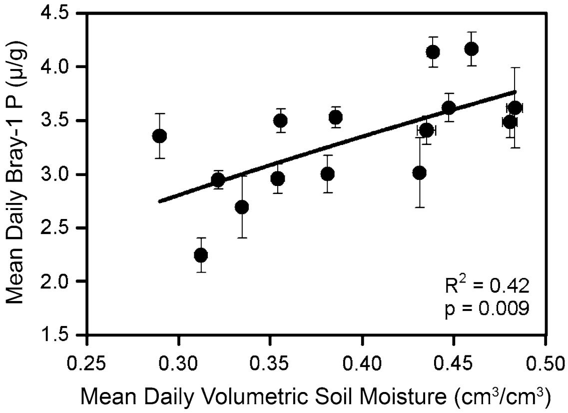

Fig. 4 Regression between labile soil P and volumetric soil moisture using mean daily values for each of the three plots

Discussion

Contrary to expectations, labile P did not vary significantly on hourly time-scales with the exception of the 24-h sample period (Fig. 2e). Our finding of significant variation in labile soil P on Day 5, but not the other days, could have occurred because we sampled over a longer time-frame, thus capturing a broader pattern of change in labile soil P (Fig. 2; Wood et al. 2013). These results would suggest that the primary dominant factors controlling labile soil P at this site vary on daily and not hourly time-scales. That we found no significant diurnal variation of soil respiration, temperature or soil moisture in this forest supports this supposition (Wood et al. 2013). All in all, our results are in direct contrast to a similar study conducted in a wet tropical forest in Costa Rica (Vandecar et al. 2009). In the Costa Rican study, labile soil P did vary significantly throughout the day and the diurnal pattern was characterized by a bimodal curve, with a low point occurring midday. Furthermore, while labile soil P in our site was strongly controlled by soil moisture availability (Fig. 3), 86 % of the variability in labile P of the Costa Rican forest was explained by soil CO_2 efflux, soil temperature and sap flow, such that labile P increased with soil CO_2 efflux and soil temperature and decreased with increased sap flow, with no relationship between labile soil P and soil moisture. However, given that total soil respiration represents fluxes from multiple sources (e.g. heterotrophs feeding on organic matter as well as autotrophic respiration), each of which may have different temperature or moisture responses (Subke et al. 2006), it is difficult to ascertain whether labile soil P would have varied with soil CO_2 efflux had we partitioned respiration into its various components. Nevertheless, the contrasting results led us to ask why these two forests might have differed both in the time-scale over which labile soil P varies and in the dominant factors that control this variability.

Both the forest in Puerto Rico and the forest in Costa Rica are wet tropical forests located on highly weathered tropical soils with low intra-annual variability in temperature (Heartsill-Scalley et al. 2007; Vandecar et al. 2009). One theory as to why P varied significantly on a diurnal time-scale in Costa Rica, but not in Puerto Rico, is the difference in the level of soil saturation. In Costa Rica, the volumetric soil moisture ranged from 58 to 68 % (Vandecar et al. 2009), while at the Puerto Rican site, volumetric soil moisture ranged from 34 to 45 %. Over the course of this study, the Puerto Rican forest is likely to have experienced some level of moisture limitation (Fig. 1). This hypothesis is supported by the positive effect of soil moisture on labile soil P in this forest, which tends to vary more strongly on daily rather than hourly time-scales (Wood et al. 2013), and by the lack of a significant relationship between soil moisture and labile soil P in the Costa Rican Forest (Vandecar et al. 2009). Furthermore, an experimental drought established in this same forest site resulted in a significant decline in labile soil P (Wood and Silver 2012). The negative relationship between soil moisture and labile soil P over the 24-h period (Day 5) occurred on the driest day. This negative relationship between labile soil P and moisture could have resulted from low transport of P through the soil matrix in especially dry soils, thus reducing plant and microbial access to the available soil P pool (Allison 2005; Stark and Firestone 1995). In wet tropical forests with no marked dry season, like Luquillo, dry spells can cause lysis of microbial biomass, which would also lead to higher levels of labile soil P during dry periods (Lodge et al. 1994; Sparling et al. 1987).

Another important difference between the Puerto Rican and the Costa Rican forests is the degree of diurnal variation in temperature. The forest in Puerto Rico experiences much lower variation in temperature relative to the Costa Rican forest (5 vs 8 °C, respectively; Vandecar et al. 2009). Thus, the lack of a relationship between labile soil P and soil temperature in this forest might be because the change in temperature over the course of this study was not large enough to drive changes in the labile soil P pool. Furthermore, moisture availability can limit the positive effect of temperature on biological processes. For example, in this forest we found a significant positive relationship between soil temperature and soil CO_2 efflux on seasonal time-scales; however, this positive effect disappeared when soil moisture was significantly reduced (Wood et al. 2013). Thus, it is likely that temperature positively influences labile soil P in this forest when moisture is not limiting. Finally, while the aboveground biomass of the forest in Costa Rica is similar to that of the Puerto Rican forest (~160 Mg/ha; Clark and Clark 2000; Cusack et al. 2010), the concentration of labile soil P is much lower in Costa Rica (0.8–2.5 vs 2.8–3.8 μg/g, respectively). In our study site, the dominant species is the palm, *P. montana*, which has been linked with both higher foliar and labile soil P (Scatena 1989; Wood and Silver 2012). That the one plot that was dominated by a dicotyledonous woody plant had lower available soil P than the two plots dominated by the *P. montana*, would support the potential role that species composition has on available soil P. However, separating environmental controls on species composition versus the effect of species on the environment is difficult to separate due to the tendency of many of these factors to co-vary. Nevertheless, the lower concentrations of labile soil P in the Costa Rican forest may have resulted in a much stronger biological demand for P relative to the Puerto Rican forest. Whether species composition can be linked to these differences is deserving of additional research.

Labile soil P in this Puerto Rican forest varies significantly on daily time-scales over a period of several weeks and that variation is largely driven by soil moisture. The range of labile soil P concentrations differed as much as 31 % across the five sample days. We would therefore recommend researchers control for soil moisture and the timing of precipitation events when measuring labile soil P stocks in this forest. Results from this study also highlight the strong possibility that the dominant factors controlling P cycling, and potentially other biogeochemical processes, in tropical forest soils can differ significantly among tropical forest sites, despite strong similarities in climate and soil type.

Acknowledgments We would like to thank Dr. Ariel E. Lugo and Dr. Whendee L. Silver for their invaluable support. We additionally thank C. Torrens and B. Quintero who helped in the laboratory and the field. Support for this research was provided by a NOAA Climate and Global Change Postdoctoral Fellowship to TEW and a University of Virginia College of Arts & Sciences Small Research and Travel Grant to DM. This research was additionally supported by the USDA Forest Service International Institute of Tropical Forestry as part of the Long Term Ecological Research Program.

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