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Phosphorus fractionation in lowland tropical rainforest soils in central Panama

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ABSTRACT

Phosphorus availability is commonly assumed to limit productivity in lowland tropical rainforests, yet there is relatively little information on the chemical forms of soil phosphorus in such ecosystems. We used the Hedley sequential fractionation scheme to assess phosphorus chemistry in five soils supporting tropical rainforest on Barro Colorado Island, Republic of Panama. The soils represented a range of orders (Inceptisols, Alfisols, and Oxisols) formed on contrasting geological substrates and topography, but under uniform climate and vegetation. Total phosphorus in surface horizons ranged between 315 and 1114 mg P kg^{-1}, being lowest on a soil derived from marine sediments and highest on soils derived from andesite. The majority of the phosphorus occurred in recalcitrant forms, although between 14% and 39% occurred as organic phosphorus. Readily-available phosphate, as extracted by anion-exchange membranes, occurred in small concentrations (4–13 mg P kg^{-1}), although labile phosphorus, defined as phosphate extracted by anion-exchange membrane plus inorganic and organic phosphorus extracted by 0.5 M $NaHCO_3$, accounted for between 4.7% and 11.4% of the total soil phosphorus. Our results indicate a strong control of geology and topography on soil phosphorus in tropical rainforests, which may have important implications for understanding the diversity and distribution of plant species in such ecosystems. Further, some of the most common soils on Barro Colorado Island, including those on the 50 ha forest dynamics plot, are rich in phosphorus despite their relatively advanced stage of pedogenesis.

1. Introduction

In the preface to *Diversity of Soils in the Tropics* (Drosdoff et al., 1978), the editors lamented the widespread use of the term 'tropical soils' as an entity with common properties. In particular, this ill-conceived if enduringly popular misconception is often associated with the assumption that tropical soils contain low concentrations of available phosphorus. Phosphorus availability can certainly constrain plant productivity on strongly-weathered soils, which are common in the tropics (e.g., Cross and Schlesinger, 1995; Tanner et al., 1998). Such soils contain high concentrations of aluminium and iron oxides that fix phosphate strongly, so that a large proportion of the phosphorus occurs in sparingly-soluble crystalline or occluded forms associated with secondary minerals (Weir, 1977; Cross and Schlesinger, 1995; Tiessen, 1998). As these forms of phosphorus are of limited biological availability, phosphorus acquisition by plants growing on strongly weathered soils is regulated to a large extent by the turnover of organic phosphorus and the rapid recycling of phosphorus from litter fall (Tiessen et al., 1992; Johnson et al., 2003). This includes direct mineralization and release of phosphorus from surface root mats in the most extremely phosphorus-deficient environments (Stark and Jordan, 1978).

Although it is commonly assumed that phosphorus limits productivity in tropical forests, total soil phosphorus concentrations vary widely, with values ranging from <100 to >1400 mg P kg^{-1} (Johnson et al., 2003). Readily-extractable inorganic phosphate concentrations are usually low (<5 mg P kg^{-1}), but if the definition of labile phosphorus is broadened to include organic phosphorus in $NaHCO_3$ extracts, values can be >10-fold greater than the annual phosphorus requirement of the forest (Johnson et al., 2003).

Despite the importance of understanding nutrient cycles in tropical forests, relatively little detailed information exists on soil phosphorus fractions in such ecosystems. Although abundant information is available on soil phosphorus chemistry in tropical agricultural systems (e.g., Solomon and Lehmann, 2000; Buehler et al., 2002; Nziguheba and Bünemann, 2005; George et al., 2006), there has been no broad-scale assessment of undisturbed tropical forest soils, and data are available on only a few locations (reviewed in Johnson et al. (2003) and Negassa and Leinweber (2009)). There is also a lack of data from sub-surface horizons, because many studies have analyzed only the surface soil (often the upper 10 or 20 cm). However, there is evidence that roots of tropical trees can acquire mineral elements from deep in the soil profile (Porder et al., 2006), a

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potentially important long-term source of phosphorus for tropical forests.

Here we report data from a reconnaissance survey of soil phosphorus fractions for contrasting soil types under lowland tropical forest on Barro Colorado Island, Republic of Panama. These soils have developed under uniform vegetation and climate, but on contrasting lithology and topography, so they are subject to distinct mineralogy and weathering regimes. By studying these soils, we aimed to explore the extent to which soil phosphorus fractions and phosphorus availability vary with local-scale differences in lithology and topography.

2. Material and methods

2.1. Site description and soil sampling

Barro Colorado Island (BCI) is situated in Gatun Lake, central Panama (09° 09′ N, 79° 51′ W). The mean annual temperature is 27 °C and varies by only 1 °C on a monthly basis, while mean annual rainfall is 2600 mm with a four-month dry season from December to April (Windsor, 1990). The 1564 ha island supports primary and mature secondary semi-deciduous tropical moist forest (Foster and Brokaw, 1982).

The island consists principally of three geological formations: the Bohio formation, which includes volcanic and marine (conglomerate) facies (although the latter is of limited extent); the Caimito formation, which comprises volcanic and marine (foraminiferal limestone) facies; and a central plateau of andesite (Woodring, 1958; Johnsson and Stallard, 1989; Baillie et al., 2007). The topography varies from nearly flat to slightly sloping on the Caimito marine facies and andesite plateau to deeply incised with steep slopes and narrow interfluves on the Bohio formation (Baillie et al., 2007).

The soils of BCI were recently mapped and described (Baillie et al., 2007) and 21 soil classes are now recognized. For a detailed, preliminary study of phosphorus fractions we selected five of these classes (Table 1). Two of these (AVA, profile code PF01; Marron, profile code PR03) are of particular significance, because they represent the soils of the Center for Tropical Forest Science (CTFS) 50 ha forest dynamics plot on the andesite plateau in the center of the island (Leigh et al., 2004). Additional information on the five soil classes is available online, including profile descriptions and details of soil chemistry, morphology, and mineralogy (Baillie et al., 2007).

At the end of dry season in 2007, soil profile pits were cleaned and soil samples taken from previously classified genetic horizons (Baillie et al., 2007). Based on the detailed soil mapping conducted previously on BCI, the profiles were considered to be representative of the respective soil classes. Soils were air-dried for 10 d at room temperature (~22 °C and 55% humidity) and visible roots and macro fauna were removed by hand. Samples were then sieved (<2 mm) and milled to a fine powder.

2.2. Phosphorus fractionation

Triplicate 0.5 g soil samples were placed into 50 mL screw cap centrifuge plastic tubes and extracted according to the Hedley sequential extraction procedure (Hedley et al., 1982; Tiessen and Moir, 2008). A blank (no soil) and a sample of a standard laboratory soil (from a lowland tropical forest at Albrook, Republic of Panama) were included with each run.

Phosphate extracted by anion-exchange membranes (1×4 cm; manufactured by BDH, Poole, UK, and distributed by VWR International, West Chester, PA) was desorbed from the membranes by shaking for 1 h in 0.25 M H_2SO_4. All other extracts were centrifuged (8000×*g*, 15 min) and an aliquot decanted for analysis. Each aliquot was neutralized using phenolphthalein indicator and dilute NaOH or H_2SO_4 (as appropriate) and analyzed for inorganic phosphate and total phosphorus. Phosphate was determined by molybdate colorimetry (Murphy and Riley, 1962) at 880 nm with a 1-cm path length. Total phosphorus was determined by the same procedure following acid–persulfate digestion (Rowland and Haygarth, 1997) at 80 °C overnight in sealed glass tubes. In both cases, standards were prepared in the extract solution following identical neutralization and dilution steps. The detection limit for both procedures was approximately 0.6 mg P kg^{-1}. Organic phosphorus was calculated as the difference between total phosphorus and inorganic phosphate, although this will have over-estimated organic phosphorus for soil extracts containing inorganic polyphosphates, which are included in the organic phosphorus fraction (Turner et al., 2005).

For extracts containing organic matter, a separate aliquot of neutralized solution was measured without molybdate reagent (i.e., containing acid only) to correct for color interference. An alternative procedure involves precipitation of organic matter by acidification, but this was considered more time-consuming than analyzing a control solution and initial tests indicated that results were similar for both procedures. The $NaHCO_3$ extracts were initially acidified with 0.5 mL of 3 M H_2SO_4 to remove carbonates prior to addition of the molybdate reagent (Turner and Haygarth, 2003).

2.3. Determination of soil properties

Total soil phosphorus was determined independently of the Hedley fractionation procedure by ignition (550 °C, 1 h) and extraction in 1 M H_2SO_4 (1:50 soil to solution ratio, 16 h), with phosphate detection by automated molybdate colorimetry using a Lachat Quickchem 8500 (Hach Ltd, Loveland, CO). This procedure gave quantitative recovery of total phosphorus from a certified reference soil (Loam D, High Purity Standards, Charleston, SC) and a similar value for the laboratory standard soil when compared to a H_2O_2–H_2SO_4 digestion procedure. Soil pH was measured in deionized water (1:2 soil to solution ratio) using a glass electrode. Amorphous aluminium (Al_{ox}) and iron (Fe_{ox}) were determined by extraction in a solution containing ammonium oxalate and oxalic acid for 2 h in the dark (Loeppert and Inskeep, 1996) with detection by inductively-coupled plasma optical-emission spectrometry (ICP-OES) using an Optima 2100 (Perkin-Elmer Inc., Shelton, CT). Total carbon and nitrogen were determined by combustion and gas chromatography using a Flash NC1112 Soil Analyzer (CE Elantech, Lakewood, NJ).

2.4. Data analysis

Phosphorus fractions are expressed as the arithmetic mean of the three replicate extracts and are concentrations in mg P kg^{-1} of the fine earth (<2 mm) fraction. All results are expressed on the basis of oven-dried soil (105 °C, 24 h). The concentrations of Al_{ox} and Fe_{ox} in each

Table 1
Genetic and morphological classification and location of sampled profiles on Barro Colorado Island, Republic of Panama (Baillie et al., 2007). The soils are ranked in order of their total phosphorus concentrations in surface samples (see Table 2).

Soil class (profile code)	Geology	Soil morphological type	U.S. soil taxonomy	Topography
Barro Verde (PR01)	Caimito marine sedimentary	Pale swelling clay	Aquertic Hapludalf	Undulating
Wetmore (PR08)	Caimito marine sedimentary	Brown fine loam	Typic Eutrudept	Strongly dissected
Hood (PR09)	Caimito volcanic	Brown fine loam	Typic Eutrudept (–Eutrudox)	Undulating
Marron (PR03)	Andesite	Brown fine loam	Mollic–Typic Eutrudept (–Eutrudox)	Stepped
AVA (PF01)	Andesite	Red light clay	(Hapludalfic) Typic Eutrudox	Nearly flat