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SOIL PHOSPHORUS

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11 Soil Phosphorus Cycling in Tropical Soils: An Ultisol and Oxisol Perspective

Sasha C. Reed and Tana E. Wood

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11.1 INTRODUCTION

Phosphorus (P) is essential for life. It is the backbone of our DNA, provides energy for biological reactions, and is an integral component of cell membranes. As such, it is no surprise that P availability plays a strong role in regulating ecosystem structure and function (Wassen et al. 2005; Elser et al. 2007; Condit et al. 2013) and in determining our capacity to grow food for a burgeoning human population (Sharpley et al. 1997; Sims and Sharpley 2005; Lal 2009). Concerns that P supplies are insufficient to meet growing demands of our species are on the rise (Tiessen 2001; Cordell et al. 2009; Richardson and Simpson 2011), and scientific and media outlets increasingly discuss P as an element worthy of our attention and concern (e.g., Cordell et al. 2009; Loughheed 2011; Edixhoven et al. 2013; Ulrich et al. 2013). Indeed, a number of groups are calling for the explicit stewardship of our planet's P stocks (Schipper 2014; Withers et al. 2015). Yet a focus on P as a vital and limited resource is not new in the tropics, where an abundance of soils characterized by low P has resulted in

TABLE 11.1

Soil Taxonomy Order Distribution^a within the Tropics^b and Average Soil P Pool Sizes for Those Orders as Determined by the Hedley Fractionation Method

Order	Tropical		Resin Inorganic P (mg/kg)	Bicarbonate Inorganic P (mg/kg)	Bicarbonate Organic P (mg/kg)	Apatite P (mg/kg)	Total P (mg/kg)
	10 ⁶ (ha)	Percentage (%)					
Entisols	1276	26.8	40.27 ± 9.63 (<i>n</i> = 9)	27.62 ± 9.93 (<i>n</i> = 9)	284.19 ± 46.80 (<i>n</i> = 9)	18.33 ± 6.51 (<i>n</i> = 8)	579.68 ± 30.05 (<i>n</i> = 9)
Inceptisols	470	9.9	35.90 ± 9.88 (<i>n</i> = 9)	13.98 ± 3.26 (<i>n</i> = 9)	63.96 ± 23.94 (<i>n</i> = 9)	41.04 ± 11.68 (<i>n</i> = 9)	491.71 ± 89.58 (<i>n</i> = 9)
Andisols	48	1.0	63.33 ± 40.92 (<i>n</i> = 3)	36.62 ± 6.57 (<i>n</i> = 13)	179.61 ± 30.98 (<i>n</i> = 13)	39.69 ± 6.52 (<i>n</i> = 13)	903.07 ± 107.80 (<i>n</i> = 13)
Histisols	31	0.7	38.68 ± 12.45 (<i>n</i> = 5)	23.06 ± 4.05 (<i>n</i> = 5)	28.88 ± 14.06 (<i>n</i> = 5)	87.00 ± 26.55 (<i>n</i> = 4)	628.60 ± 134.17 (<i>n</i> = 5)
Gelisols	1	0.0					
Aridisols	376	8.0	22.12 ± 4.78 (<i>n</i> = 14)	13.52 ± 2.69 (<i>n</i> = 14)	244.57 ± 35.78 (<i>n</i> = 14)	5.27 ± 1.49 (<i>n</i> = 8)	411.54 ± 64.18 (<i>n</i> = 14)
Vertisols	206	4.4	19.80 ± 5.44 (<i>n</i> = 5)	14.80 ± 7.07 (<i>n</i> = 5)	212.60 ± 75.19 (<i>n</i> = 5)	6.75 ± 0.85 (<i>n</i> = 4)	497.00 ± 95.00 (<i>n</i> = 5)
Mollisols	48	1.0	19.33 ± 1.81 (<i>n</i> = 43)	11.49 ± 0.99 (<i>n</i> = 43)	169.05 ± 11.53 (<i>n</i> = 39)	19.12 ± 3.46 (<i>n</i> = 40)	552.77 ± 23.33 (<i>n</i> = 43)
Alfisols	561	11.9	15.11 ± 2.99 (<i>n</i> = 17)	13.15 ± 2.97 (<i>n</i> = 17)	78.92 ± 15.61 (<i>n</i> = 17)	14.71 ± 2.43 (<i>n</i> = 17)	364.74 ± 37.01 (<i>n</i> = 17)
Spodosols	5	0.1	18.45 ± 2.48 (<i>n</i> = 11)	15.54 ± 2.12 (<i>n</i> = 11)	30.84 ± 13.51 (<i>n</i> = 6)	27.87 ± 4.56 (<i>n</i> = 11)	292.90 ± 38.86 (<i>n</i> = 11)
Ultisols	757	16.0	6.80 ± 1.08 (<i>n</i> = 38)	5.85 ± 0.72 (<i>n</i> = 38)	7.36 ± 1.64 (<i>n</i> = 38)	11.66 ± 1.19 (<i>n</i> = 38)	225.18 ± 21.77 (<i>n</i> = 38)
Oxisols	956	20.2	3.62 ± 0.47 (<i>n</i> = 11)	10.15 ± 5.66 (<i>n</i> = 14)	0.90 ± 0.22 (<i>n</i> = 14)	8.12 ± 1.69 (<i>n</i> = 13)	193.35 ± 35.39 (<i>n</i> = 14)
Total	4726	100.0					

Source: Palm, C., Sanchez, P., Ahamed, S., and Awiti, A., *Annual Review of Environment and Resources*, 32, 99–129, 2007; Yang, X., and Post, W. M., *Biogeosciences*, 8, 2907–2916, 2011. With permission.

Note: Values shown are means ± standard error, and the number of values comprising the mean is shown in parentheses.

^a Estimates exclude areas not covered by soils (e.g., rocks, water bodies, shifting sands, ice).

^b Definitions: tropical, <23.5°; temperate zone, 23.6°–60°; boreal, >60°.

a substantial, long-standing reliance on P inputs for tropical ecosystem function in both unmanaged and agricultural settings (Table 11.1, Figure 11.1; Sanchez 1976; Swap et al. 1992; Chadwick et al. 1999; Okin et al. 2004; Lal 2009). Indeed, there is a long history of cultivation in the tropics, where for thousands of years land management practices have included methods that effectively modify P availability for plant growth (e.g., Sanchez 1976; Giardina et al. 2000; Lawrence and Schlesinger 2001; Vitousek et al. 2004; Tiessen et al. 2005; Lewis et al. 2015). Nevertheless, low soil fertility in tropical systems where fertilizer is scarce has long been recognized as a major source of hunger and starvation (Sanchez and Buol 1975; Sanchez 2002; Sanchez and Swaminathan 2005; Vitousek et al. 2009).

In addition to supporting the majority of the world's population (Vira et al. 2015) and biodiversity (Myers et al. 2000), tropical ecosystems store and exchange enormous amounts of energy and carbon (C) with the atmosphere (Brown and Lugo 1982; Foley et al. 2003; Beer et al. 2010; Pan et al. 2013). Accordingly, tropical ecosystems maintain a vast potential to create feedbacks to future climate at the global scale, and there is a growing interest in understanding P cycling interactions with tropical forest responses to environmental change (Silver 1998a; Townsend et al. 2011; U.S. Department of Energy 2012; Yang et al. 2014; Cavaleri et al. 2015; Reed et al. 2015).

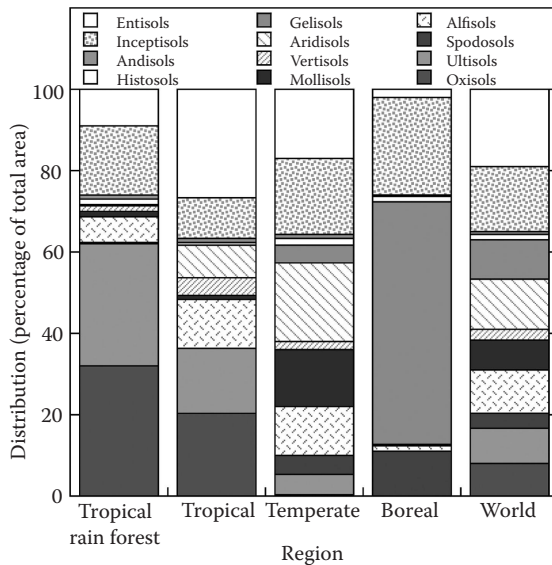


FIGURE 11.1 (See color insert.) Distribution of soil orders among tropical/subtropical moist broadleaf forests (rain forests), all tropical, temperate, and boreal ecosystems, as well as globally. Estimates exclude areas not covered by soils (e.g., rocks, water bodies, shifting sands, ice), and soil order classifications are based on the USDA soil taxonomy system (Soil Survey Staff 1998). The sequence of the soil orders is arranged from less well-developed soils (upper part of the graph; e.g., Entisols) to more well-developed soils (lower part of the graph; e.g., Oxisols). Tropical areas are defined as $\leq 23.5^\circ$, temperate areas as 23.6° – 60° , and the boreal zone as $>60^\circ$. All data are from Palm et al. (2007), who determined the extent of the 12 soil orders of soil taxonomy and their geographical distribution using the USDA's Global Soil Regions dataset.

Now is an exciting time to evaluate our understanding of tropical P cycling in this context of change (e.g., climate change, land use change), and along with highlighting the diversity in tropical P cycling and synthesizing the fundamental aspects of the tropical P cycle in Ultisols and Oxisols, this is our goal for the chapter. In the coming sections, we will discuss the multiplicity of tropical soils, dive into soil chemical P cycling on numerous timescales, consider how P affects and is affected by tropical biota, and highlight considerations of P cycling and the interactions with other biogeochemical cycles in a framework of global change.

11.2 SOIL DIVERSITY AND PHOSPHORUS CYCLING IN THE TROPICS

The tropics is a region that encircles the equator, delineated in the north by the Tropic of Cancer ($23^{\circ}26'14.0''$ N) and in the south by the Tropic of Capricorn ($23^{\circ}26'14.0''$ S; Figure 11.2). These latitudes correspond with the planet's axial tilt, and the tropics include the areas of earth where the sun reaches a point directly overhead at least once during the solar year. While we often think of a *tropical climate* as being warm and wet, in reality, the tropics maintain a myriad of climates. For example, the tropics comprise not only earth's wettest ecosystems (e.g., rain forests near Lloró, Colombia, which average 12,892 mm of precipitation/year), but also its driest (the Atacama Desert, averaging 15 mm/yr). The temperature is also highly variable, and in conjunction with this large range in climate, biota and edaphic conditions greatly vary across the tropics. In fact,

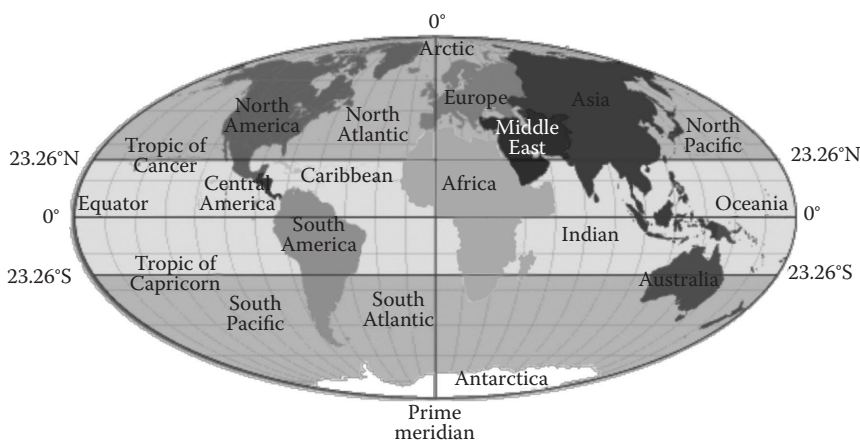


FIGURE 11.2 Global map outlining the region between 23.26° latitude north (the Tropic of Cancer) and 23.26° latitude south (the Tropic of Capricorn). The lands within these bounds are known as the *Tropics* and include all of Central America, the Caribbean, and large portions of South America, Africa, Asia (particularly India, Southeast Asia, and Indonesia), and Australia.

of the 116 Holdridge life zones (a global bioclimatic classification scheme), the tropics contain more than the sum of all the other geographic regions combined (Holdridge 1967). The tropics contain hyperdiverse wet forests, arid deserts, alpine ecosystems, dry forests, wetlands and peat lands, and many other ecosystem types. In this way, there is no representative tropical ecosystem or tropical soil (Hilgard 1906; Sanchez and Buol 1975; Richter and Babbar 1991) nor any singular tropical P cycle.

Beyond the variations in climate, soil diversity in the tropics is driven by an extremely wide variety of parent materials, biota, landforms, geomorphic characteristics, and soil ages—the variation in these factors, each of which affects soils, is greater in the tropics than in the temperate zone (Sanchez 1976; Vitousek 1984; Richter et al. 1985; McGroddy et al. 2004; Porder et al. 2007; Townsend et al. 2008). The tropics maintain all 12 soil types of the USDA soil taxonomy system (Table 11.1, Figure 11.2; Natural Resources Conservation Service 2005; Palm et al. 2007), although Gelisols are notably rare. Moreover, while the number of soil types does not differ between tropical and temperate ecosystems, the relative abundance of particular soil types is quite distinct (Figure 11.2). For example, the tropics have a much lower abundance of fertile Mollisols (e.g., the soil that supports the “breadbasket” of America), as well as a much higher abundance of highly weathered Oxisols and Ultisols. This chapter focuses on these two soil orders that make up 36% of total tropical land area (16% and 20% of global soils, respectively; Palm et al. 2007). In addition, these two soil types comprise 62% of tropical rain forests, a biome that accounts for 17% of earth’s land area and plays a disproportionately large role in global biogeochemical cycles (Palm et al. 2007; Townsend et al. 2011). Interestingly, these two prevalent soil types represent the latest stages of the soil pedogenic spectrum, which makes sense, as the extended time since glaciation and the relatively warm and wet climates found in many tropical forests are factors that result in highly weathered soils (Figure 11.3).

11.3 SOIL PEDOGENESIS AND THE DEVELOPMENT OF TROPICAL PHOSPHORUS CYCLES

Because all soil types are represented in the tropics (Table 11.1), models of soil development (pedogenesis) provide a powerful foundation on which to consider tropical soil P cycling and with which to contextualize the unique characteristics of highly weathered soils. In 1941, Jenny proposed five state factors that interact to determine the nature of a soil. This was captured in the iconic equation: $s = f(cl, o, r, p, t)$, where the state of the soil system (s) is a function of climate (cl), organisms (o), relief (r), parent material (p), and time (t) (Jenny 1941). It has been stated that P is perhaps the key element of soil pedogenesis (Walker 1965), because a parent material is P’s central source and because of P’s ecological significance (Tiessen et al. 1984; Elser et al. 2007; Vitousek et al. 2010). In contrast to the cycles of C and nitrogen (N), which have significant gaseous components, the gaseous phase of P (phosphine gas [PH_3]) is notably rare. Phosphine gas has been measured under highly anaerobic conditions,

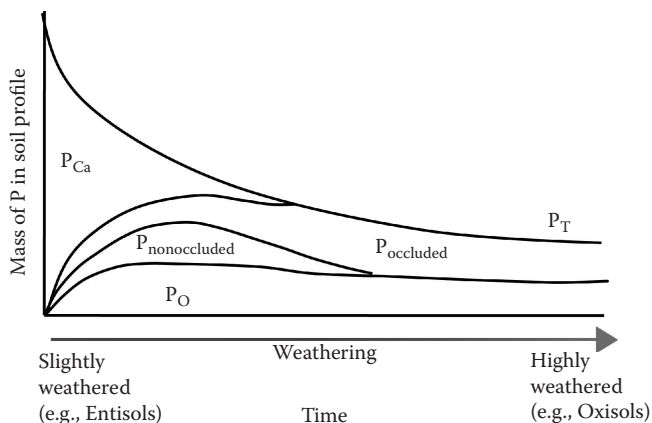


FIGURE 11.3 Graphical representation of the changes in the relative abundance of different soil P pools over the course of soil development. P_T = total soil P; P_{Ca} = calcium phosphates; P_O = organic P; $P_{occluded}$ = sorbed P (relatively unavailable to organisms); $P_{nonoccluded}$ = P in the soil solution (relatively available to organisms; often called labile P). The extent of weathering is driven by climate, type and abundance of organisms, topography, parent material characteristics, and amount of time weathering has occurred. Disturbances can also affect the rate and the nature of pedogenic change. The graphic is built of data from four soil chronosequences and shows that highly weathered soils (e.g., Oxisols) have less total P, higher relative proportions of $P_{occluded}$ and P_O , and very little available P ($P_{nonoccluded}$) relative to soils at earlier stages of soil development (e.g., Entisols). (Recreated from *Geoderma*, 15, Walker, T. W., and Syers, J. K., The fate of phosphorus during pedogenesis, 1–19, Copyright (1976), with permission from Elsevier; with kind permission from Springer Science+Business Media: *Phosphorus in Action*, Phosphorus cycling in tropical forests growing on highly weathered soils, 2011, 339–369, Reed, S., Townsend, A., Taylor, P., and Cleveland, C.)

such as sewage sludge, sediment soils, animal manure, marshes, and landfills; however, this form of P is thermodynamically unfavorable under most biogenic conditions and thus does not significantly contribute to the P cycle (Hanrahan et al. 2005). As such, it is the evolution and cycling of P within the soil system that plays the central role in determining soil P availability in terrestrial ecosystems (Figure 11.4).

Walker and Syers (1976) synthesized data from soil chronosequences to explore patterns in soil P pools in the context of pedogenesis and found that early in soil development, the majority of P is in primary mineral forms (Figure 11.3). As mineral P is weathered, it results in an increase in biologically available inorganic P (i.e., PO_4^{3-} ; unoccluded P). Some of this P is taken up by plants and microbes, while other P molecules are bound to secondary soil minerals with high P sorption capacities. *Sorption* broadly describes any process that removes a reactant from a solution, and P sorption represents the removal of P from the soil solution into less reactive geochemical sinks. In the highly weathered and acidic soils typical of tropical forests, crystalline and noncrystalline oxides of iron (Fe) and aluminum (Al) are considered the main geochemical sinks of PO_4^{3-} (Parfitt et al. 1975; López-Hernández 1977; Schwertmann and Taylor 1977; Parfitt 1978; Hsu 1989). In contrast,

P mineralization—the conversion of organic P to inorganic P—returns organic P (as created by plants and microbes) to inorganic pools, which can then be readily utilized by the biota, sorbed onto the soil surfaces, or remain within the soil solution (Figures 11.4 and 11.5). Much of the variability in unoccluded P can be accounted for by organic forms of P, which suggests that P mineralization may be a major determinant of P fertility in these soils (Tiessen et al. 1984). Each turn of the P cycle can lead to P being sorbed to soil surfaces, precipitated, and/or lost via leaching in both organic and inorganic forms (e.g., Hedin 1995). Thus, as soil development reaches more advanced stages (i.e., Ultisols and Oxisols), the total amount of P in the system declines, and much of the P that is left is bound, insoluble, or physically protected in occluded forms (Table 11.1; Figure 11.3).

This decline over time in P obtained from parent material increases the relative importance of soil P inputs that occur from atmospheric dust and mineral aerosol deposition (Swap et al. 1992; Chadwick et al. 1999; Okin et al. 2004; Pett-Ridge 2009). Phosphorus can be transferred through the atmosphere over extremely long distances in the form of dust (Swap et al. 1992; Chadwick et al. 1999; Okin et al. 2004; Mahowald et al. 2005; Pett-Ridge 2009) and as ash from local biomass burning (Mahowald et al. 2005; Das et al. 2013). The importance of dust inputs to tropical ecosystems depends on the existing reservoir of P as well as the flux of dust being transported and deposited. Multiple studies suggest that atmospheric P inputs

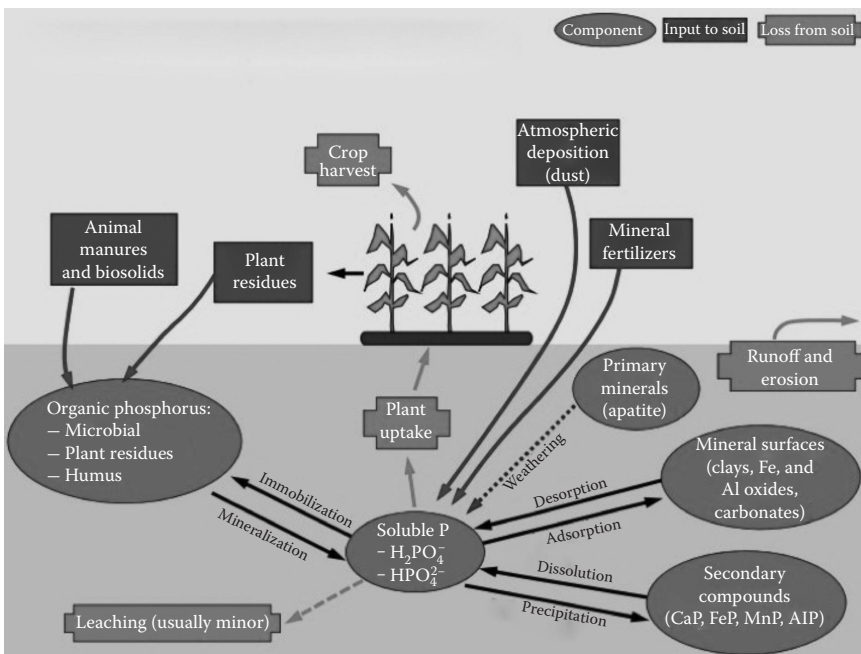


FIGURE 11.4 (See color insert.) The P cycle, focusing on P pools (green ovals), inputs (blue rectangles), and loss (orange polygons). (Reproduced with permission from Wikipedia Creative Commons, en.wikipedia.org/wiki/Phosphorus_cycle.)

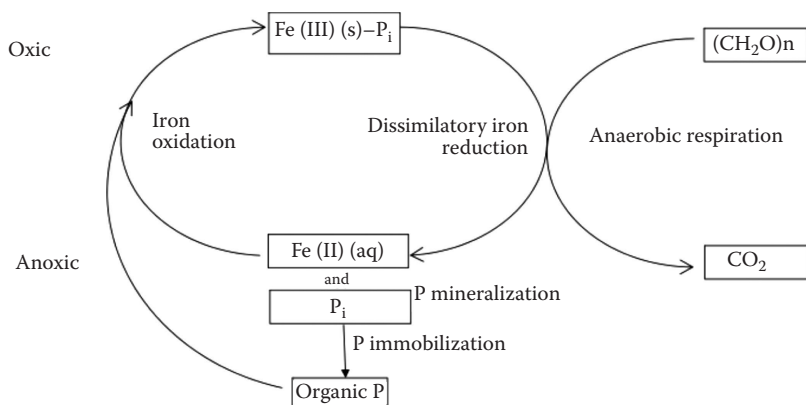


FIGURE 11.5 Conceptual model from Liptzin and Silver (2009) showing the relationship between Fe, O₂, P availability, and carbon oxidation. During more anoxic periods (e.g., following precipitation events), bacteria reduce Fe (III) to Fe (II), oxidizing organic C into CO₂. At the same time, Fe-bound inorganic P (P_i) is released and may be quickly immobilized by roots and/or microbes. During periods when O₂ availability is higher, Fe (II) is oxidized to Fe (III) via biotic and/or abiotic reactions, and the Fe (III) oxides are again available to bind inorganic P. (Reprinted from *Soil Biology and Biochemistry*, 41, Liptzin, D., and Silver, W. L., Effects of carbon additions on iron reduction and phosphorus availability in a humid tropical forest soil, 1696–1702, Copyright (2009), with permission from Elsevier.)

to tropical forests may be critical for maintaining ecosystem productivity (Artaxo et al. 1988, 2002; Swap et al. 1992; Chadwick et al. 1999; Ben-Ami et al. 2010; Das et al. 2013). For example, some estimates have suggested that the high productivity of the Amazon rain forest is fueled, at least in part, by dust inputs originating from the Sahara/Sahel region in Africa (e.g., P inputs estimated at 1–4 kg/ha year; Swap et al. 1992). From a P pool perspective, dust inputs act to counteract the P-depleting effects of long-term weathering (Figure 11.4). Landscape dynamics can also counteract the P depletion of surface soils that are long removed from original parent material sources, resulting in higher quantities of rock-derived nutrients than would otherwise be predicted. In particular, geomorphic processes such as erosion and tectonic uplift have a strong potential to affect soils in general and tropical soil P cycling in particular. Erosion and tectonic uplift can rejuvenate such soils by bringing the parent material to the surface (Vitousek et al. 2003; Bern et al. 2005; Porder et al. 2007), and tropical ecosystems have some of the highest erosion and uplift rates on earth (White et al. 1998; Porder et al. 2007).

The chemistry of weathered tropical soils affects the mobility of soil P in unique ways. Both organic and inorganic forms of P are susceptible to sorption (e.g., Berg and Joern 2006), but the extent of this sorption is primarily influenced by soil mineralogy and the concentration, the chemistry, and the solubility of soil P (Smyth and Sanchez 1982; Singh and Gilkes 1991; Iyamuremye et al. 1996; Guppy et al. 2005; Reed et al. 2011a), as well as the competition with biological sinks (Uehara and Gillman 1981; Sollins et al. 1988; Olander and Vitousek 2004). In particular, the prevalence of 1:1 clays (e.g., kaolinite) and high concentrations of Al and Fe oxides

and hydroxides, which have a high affinity for P, are an interesting characteristic of many highly weathered tropical soils (Sanchez 1976; Harrison 1987; Sollins et al. 1988). Variable-charge clays maintain an electric charge that results from the protonation and the deprotonation of surface hydroxyl groups (Gillman 1984; White and Zelazny 1986), which occur at the edge of the 1:1 clays and Al and Fe hydroxides that dominate these soils. The charge of clay soils depends upon the soil pH, whereby small changes in pH can significantly affect the net charge of the soil and thus the mobility of anions and cations (Sollins et al. 1988). Accordingly, the mobility of P in highly weathered soils varies with soil pH, and unoccluded P may be less mobile in Ultisols and Oxisols than in soils dominated by clays with more permanent charge because permanent-charge clays typically maintain net cation exchange capacity (Gillman 1984). Fertilization studies on these soils have found high potential for P to be rapidly and nearly completely sorbed to the soil surfaces over short timescales (e.g., Sanchez 1976; Uehara and Gillman 1981; Oberson et al. 1997). Consequently, the concentrations of sorbed P often exceed that of P in the soil solution by several orders of magnitude (Sanchez 1976). However, while the process of P retention by Fe and Al oxides has been historically thought to exhibit low reversibility in highly weathered tropical soils, fluctuating redox potential common in the humid tropics can reduce Fe oxides when in the presence of labile C and humic substances. Such reduced soil conditions favor the remobilization of the geochemical or occluded pool of P, making this P once again biologically available (Figure 11.5; Chacon et al. 2006; Liptzin and Silver 2009).

The highly weathered, finely textured clay Ultisols and Oxisols that are high in Fe and Al oxides, combined with the high rainfall typical of the humid tropics, can limit the diffusive transport of oxygen (O_2). These circumstances lead to rapid fluctuations between reducing (low O_2) and oxidizing (high O_2) conditions (Silver et al. 1999; Shin 2005), which have the potential to release C and P that has been sorbed to the soil surfaces (Figure 11.5; Chacon et al. 2006; Liptzin and Silver 2009). There are several mechanisms that result in the release of P from geochemical pools under reducing conditions (Ponnamperuma et al. 1967; Gambrell and Patrick 1978; Chacon et al. 2006), which stem from bacteria obtaining energy by coupling the oxidation of organic matter (OM) to the reduction of different electron acceptors. Under anaerobic conditions, Manganese (Mn) and Fe oxides are the primary electron acceptors in soils (Lovley 1991). For example, as Fe oxides are converted to reduced forms, the phosphate anions chemically associated to Fe oxides are released (Figure 11.5; Baldwin and Mitchell 2000). Iron reduction is primarily fueled by the availability of organic acids of low molecular weight such as acetate (Kusel et al. 2002). While more complex organic substrates can also be used by Fe oxide reducers, it has been suggested that a very small percentage of these compounds and their reducing equivalents (less than 5%) are converted to Fe oxide (Lovley 1991). Humic substances also affect the patterns of Fe reduction and reoxidation in soils, whereby humic substances and quinones (oxidized derivatives of aromatic compounds) are used to shuttle electrons between electron donors and acceptors (Lovley et al. 1998). A high availability of labile C (C that is easily biologically available) combined with an abundance of the Fe-reducing bacteria typical of wet tropical forests is likely to stimulate these reactions (Liptzin and Silver 2009; Dubinsky et al. 2010). In summary,

the microbial reduction of Fe oxide can be an important mechanism for increased bioavailability of soil P in tropical forest soils (Figure 11.5; Chacon et al. 2006). There are also growing datasets that suggest that plants and soil microbes are able to directly access occluded P (Tiessen et al. 1984; Olander and Vitousek 2004; Richter et al. 2006). Regardless of the cause, the transfer of even modest amounts of P from the geochemical pool (i.e., occluded) to the soil solution can play an important role in maintaining soil P bioavailability (Chacon et al. 2006; Liptzin and Silver 2009).

McGill and Cole (1981) proposed a framework for OM decomposition that suggests P mineralization may also be largely decoupled from the mineralization of C and N. Within OM molecules, C and N are intricately bound (Asner 1997), but P is bound by phosphate ester bonds that phosphatase enzymes can independently mineralize. In this way, whether organisms mineralize organic substrates to obtain energy (in the form of reduced C) or N, mineralization of both elements occurs. In contrast, linkages between P limitation, phosphatase production, and P mineralization may be more direct because P mineralization can be relatively independent from the mineralization of C and N. Importantly, this decoupling may be particularly prevalent on highly weathered P-poor soils (McGill and Cole 1981).

Overall, the spatial heterogeneity of tropical forest soils can be viewed at two levels of organization: the geographic scale of hundreds to thousands of hectares (as described earlier) and the scale of landforms and patches that exist within this larger landscape (Webb et al. 1972; Scatena and Lugo 1995). At this finer spatial scale, local topography and drainage can substantially influence many soil characteristics that influence soil P availability, such as soil pH, soil organic matter (SOM), and exchangeable Fe (Figure 11.5). Research in tropical montane forests and in tropical forest watersheds suggests that higher landscape positions (e.g., ridge tops) are typically characterized as having higher SOM, lower pH, and higher concentrations of extractable Fe than lower topographic positions (e.g., valleys; Scatena and Lugo 1995). This variability in soil characteristics with topographic position can interact to affect soil P availability in complex ways. For example, in a wet tropical forest in Puerto Rico, soil P availability in the surface soils (0–10 cm) is correlated with forest age and not topographic position, and thus at this depth, P is likely primarily controlled by biological processes (Silver 1994; Scatena and Lugo 1995). However, when deeper profiles are considered (0–60 cm), the topographic position is the dominant control, with significantly higher biologically available soil P in valleys relative to the ridge tops (Scatena and Lugo 1995). Correlations between soil P availability and topographic position for the deeper profiles likely occur due to prevention of phosphate adsorption by organic anions (Fox 1982) and more acidic and oxic conditions in the higher topographic positions (ridges). In contrast, the lower topographic positions (valleys) likely experience altered P adsorption in soils with low Fe concentrations, more reducing conditions, and greater transport of P from higher topographic positions (Scatena and Lugo 1995). Taken together, these processes interact to increase the relative size of the P pool in subsoils located at lower topographic positions relative to higher positions (Silver 1994; Scatena and Lugo 1995). In line with the findings in Puerto Rico, biologically available P tends to increase from high to low topographic positions (e.g., Tsui et al. 2004; Porder et al. 2007; Werner and Homeier 2015). Many tropical species are often correlated with specific topographic

positions (Scatena and Lugo 1995), and foliar P concentrations also correlate with soil P variation across the landscape (Wood et al. 2006). Teasing apart the controls of geomorphology on the distribution of plants versus the effects of plants on soil P availability remains a significant challenge to the scientific community.

11.4 BIOLOGICAL INTERACTIONS WITH THE TROPICAL SOIL PHOSPHORUS CYCLE

11.4.1 BIOTIC STRATEGIES FOR ACQUIRING AND UTILIZING SOIL PHOSPHORUS

Soils are not the only component of ecosystems to evolve over long periods: organisms in tropical environments growing on P-poor soils have developed a phenomenal capacity for efficiently using and acquiring P. A central reason tropical organisms are able to maintain high activity in the face of low P availability (Table 11.1) lies in the fact that organisms in general—but especially in the tropics—have evolved a number of key nutrient conservation and acquisition strategies (e.g., Clark et al. 1999; Lambers et al. 2008). These strategies can vary along the pedogenic spectrum (Vance et al. 2003; Lambers et al. 2008; Reed et al. 2011a; Turner et al. 2013a; Ellsworth et al. 2015), as well as among species (Lambers et al. 2008; Reed et al. 2012; Mayor et al. 2014; Steidinger et al. 2015; Zemunik et al. 2015), and conservation strategies include increased growth per unit P (Vitousek 1984), reallocation of internal P (e.g., foliar P resorption prior to leaf senescence; Aerts 1996; Kitayama and Aiba 2002; Yuan and Chen 2009; Wood et al. 2011; Reed et al. 2012), and modifications in metabolism to minimize P-requiring steps (e.g., alternative glycolytic reactions that bypass ATP-requiring steps [Theodorou and Plaxton 1996; Uhde-Stone et al. 2003]). Plants also have mechanisms to maximize soil P acquisition. Phosphorus is much less mobile in the soil solution than most other major plant nutrients (Barber 1984), and P uptake is often assumed to vary in proportion to the surface area of the plant uptake organs involved. Thus, low P availability can be somewhat countered via symbiotic relationships and a number of morphological adaptations that increase root surface area, including mycorrhizal relationships, root hairs, and roots with unusual architecture (Figure 11.6; Lodge 1993; Aldrich-Wolfe 2007; Jansa et al. 2011). For example, some tropical plants make use of lateral roots that scavenge P from litter layers (Herrera et al. 1978; Stark and Jordan 1978; Cuevas and Medina 1986), which contain relatively high P concentrations. Other plants produce specialized root structures (e.g., cluster roots) that allow plants to mine insoluble forms of inorganic P from the soil: cluster roots produce large amounts of carboxylates, which release P from strongly sorbed forms (Figure 11.6; Lambers et al. 2008). Cluster-rooted plants have been observed in many tropical forests, and many of the best-known cluster-rooted species are found in western Australia, in soils with some of the most weathered and P-poor soils on earth (Figure 11.6). The fungal translocation of P through hyphal connections can also play an important role in conserving P in tropical forested ecosystems (Figure 11.6; Lodge et al. 2014).

Microbial organisms, including mycorrhizae, can solubilize P from occluded inorganic pools, transforming it into available P. By releasing strong organic acids, certain bacteria can liberate P from pools that are typically thought of as biologically

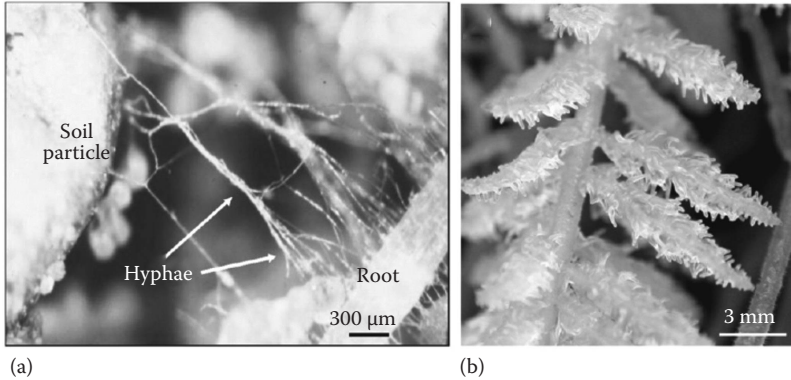


FIGURE 11.6 (See color insert.) Plant nutrient-acquisition strategies. (a) Mycorrhizal fungi extend beyond the root zone and greatly increase the volume of soil that can be explored for P uptake. All mycorrhizas (arbuscular mycorrhizas, ectomycorrhizas, and ericoid mycorrhizas) are involved in the uptake of soluble inorganic P. Photo shows the hyphae of *Glomus caledonium*, an arbuscular mycorrhizal fungus that in the picture is growing into the soil from a host root of the plant *Trifolium repens*. (Photo by Iver Jakobsen, reprinted with kind permission from Springer Science+Business Media. *Mycorrhizal Ecology*, Foraging and resource allocation strategies of mycorrhizal fungi in a patchy environment, 2003, 93–115, Olsson, P. A., Jakobsen, I., and Wallander, H.; reprinted from *Trends in Ecology and Evolution*, 23, Lambers, H., Raven, J. A., Shaver, G. R., and Smith, S. E., Plant nutrient-acquisition strategies change with soil age, 95–103, Copyright (2008), with permission from Elsevier.) (b) Root morphology helps plants access P from soil; for example, Proteaceae species that grow under extremely low P supply in highly weathered Australian soils have a number of root morphological adaptations. Shown here is a proteoid root cluster of *Banksia grandis*. (Photo by Michael W. Shane, reprinted from *Trends in Ecology and Evolution*, 23, Lambers, H., Raven, J. A., Shaver, G. R., and Smith, S. E., Plant nutrient-acquisition strategies change with soil age, 95–103, Copyright (2008), with permission from Elsevier.)

inaccessible (Bonan 1991; Bünenmann et al. 2004; Olander and Vitousek 2004; Richter et al. 2006). These results are supported by data suggesting that microbial organisms can effectively compete with geochemical sinks for soil P (Olander and Vitousek 2004). At a global scale, the C:N:P ratios of both the soil (186:13:1) and the soil microbial biomass (60:7:1) are well constrained (Cleveland and Liptzin 2007), and evidence suggests the C:N:P of microbial biomass may lend perspective into questions of nutrient limitation in terrestrial ecosystems. When OM accumulates in an ecosystem, the soil C and N concentrations become increasingly decoupled from the total soil P concentration (McGill and Cole 1981). This observation may reflect a more efficient use of P released from the cycling of organic P pools in the mineral soil and the forest floor, rather than the weathering of inorganic P from primary minerals. Organic P pools are thought to be an important source for labile P in forest soils, especially for tropical forests (Johnson et al. 2003). Measured site-specific microbial N:P ratios that diverge from the calculated average (i.e., 6.9 ± 0.4) may provide insight into the nature of nutrient limitation, at least within lowland tropical ecosystems. For example, relatively high measured microbial N:P ratios (suggesting P limitation) correspond with direct evidence that soil P availability

limits microbial biomass, activity, and other ecosystem processes in a wet tropical forest in Costa Rica (Cleveland et al. 2002; Cleveland and Townsend 2006; Reed et al. 2007; Wieder et al. 2009).

11.4.2 PLANT AND ANIMAL INTERACTIONS WITH SOIL PHOSPHORUS

We know from temperate ecosystems that different plant species have the capacity to affect the chemistry of soil in species-specific ways: temperate forest research indicates a large interspecific variation in the effects of trees on soil properties (Zinke 1962; Gersper and Holowaychuk 1971; Binkley and Giardina 1998; Finzi et al. 1998; Hobbie et al. 2006). Factors such as volume and chemistry of stemflow, nutritional requirements of trees, organic chemistry of litter, and N₂-fixing abilities affect how different tree species alter soils on micro- and mesoscales. An emerging body of work suggests that even in highly diverse tropical forests, tree species can affect the soil in which they live (Reed et al. 2008; Keller et al. 2013; Uriarte et al. 2015; Waring et al. 2015). For example, a recent study in Puerto Rico by Uriarte et al. (2015) found that most tree leaf litter fell less than 5 m from the source tree, which generated fine-scale spatial heterogeneity in leaf litter inputs, with significant implications for soil P cycling. Another study in Costa Rica observed strong correlations between canopy, litter, and soil P concentrations, such that species-specific differences in P were observable along a canopy-to-soil profile, suggesting a species-generated P footprint (Reed et al. 2008). It is important to note the likelihood not only for tree species effects on soil chemistry, but also for soils to dictate the community composition (and thus community-level plant traits) and/or chemistry of trees (John et al. 2007; Condit et al. 2013). The two possibilities are not mutually exclusive nor is it new to recognize how difficult it is to tease apart these controls. For example, in his assessments of the drivers of soil development, Jenny himself recognized the issue, saying “Like everybody else I could see that the vegetation affects the soil and the soil affects the vegetation, the very *circulus vititis* that I was trying to avoid” (Jenny 1981).

These suggestions of vertical linkages between canopy and soil chemistries are also intriguing in the context of increasing remote-sensing capacity for assessing biogeochemical patterns and functions in diverse tropical forests. If we can use remote-sensing technologies to gain information about forest floor processes, the information would not only provide insight into direct nutrient controls over foliar function (e.g., Walker et al. 2014) but could also help quantify the spatial patterns of biogeochemical cycles occurring beneath the tree crowns. This provides hope that we can continue to distill the tropical forest biogeochemical complexity represented by hundreds of species per hectare (Townsend et al. 2008).

Ecosystem controls and effects are mediated through many trophic levels. For example, in a temperate forest common garden experiment, Hobbie et al. (2006) showed significant tree species effects on litter decomposition, with data suggesting that tree species controls were occurring, in part, through interactions between calcium concentrations and earthworm abundance. We know that animals can be affected by and affect soil P pools in tropical forests (Figures 11.7 and 11.8; McGlynn et al. 2007; Sayer et al. 2010; Hong et al. 2011; Marichal et al. 2011), and animals

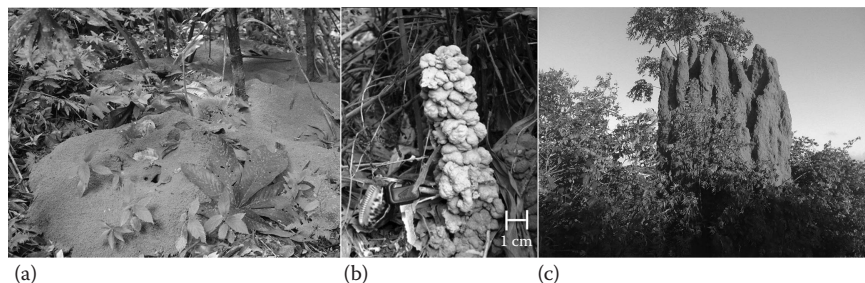


FIGURE 11.7 (See color insert.) Photos showing the effect of animal activity on soil structure. (a) *Atta cephalotes* leaf cutter ant nest in Cockscomb Basin Wildlife Sanctuary, Belize. The photo shows the massive soil translocation ants create in building their nests in highly weathered tropical soils, as they move massive amounts of soil from deeper layers to the surface. (Courtesy of Matthew Meier.) (b) An earthworm cast produced by the tropical earthworm species *Amyntas khami* (which can grow up to 50 cm in length) in a rain forest in northeastern Vietnam. Casts are clumps of digested organic matter excreted by earthworms that aggregate into large and distinctive structures. (Reprinted from *Soil Biology and Biochemistry*, 43, Hong, H. N., Rumpel, C., Henry des Tureaux, T., Bardoux, G., Billou, D., Tran Duc, T., and Jouquet, P., How do earthworms influence organic matter quantity and quality in tropical soils? 223–230, Copyright (2011), with permission from Elsevier.) (c) Tall termite hills such as this one are common in highly weathered soils in West Africa. These hills represent large changes to soil structure and, likely, biogeochemical cycling. (Reproduced with permission from Wikipedia Creative Commons, https://commons.wikimedia.org/wiki/File:Termite_hill_in_forest.jpg.)

have profound local effects on the spatial patterns in soil properties. Termites, ants, worms, and other soil fauna can mix and chemically alter vast volumes of soil material (Figure 11.7). For example, an assessment of surface soil (0–10 cm) P concentrations in a rain forest in Costa Rica suggested that ant (*Atta cephalotes*, a leaf cutter ant) mounds significantly alter extractable P pools in consistent ways (Figure 11.8). Because ants can drive substantial physical turnover of tropical soils, the effects of these organisms on tropical soil P are of significant consequence (Perfecto and Vandermeer 1993). Phosphorus can also regulate the activity of soil animals; for example, McGlynn et al. (2007) tested the effects of soil and litter nutrient stoichiometry on the invertebrate litter fauna of a Costa Rican tropical rain forest by assessing the animal densities from 15 sites across a P gradient. There was a significant variation in the density of the invertebrate litter fauna, which was strongly tied to soil and litter P concentrations: an increase in P concentrations related to an equally large increase in animal density. Interestingly, in a study of 87 species of rain forest ants, Kaspari et al. (2015) found that the P content of the ants was strongly correlated with the organisms' thermal tolerance. It has been hypothesized that ants active at high temperatures invest in P-rich machinery to buffer their metabolism against thermal extremes, and the P content of the ants varied threefold, with a temperature sensitivity that was lower and a thermal range that was higher in P-rich ant species. An improved understanding of how plants, soils, and animals interact in tropical forests to regulate P cycling is greatly needed.

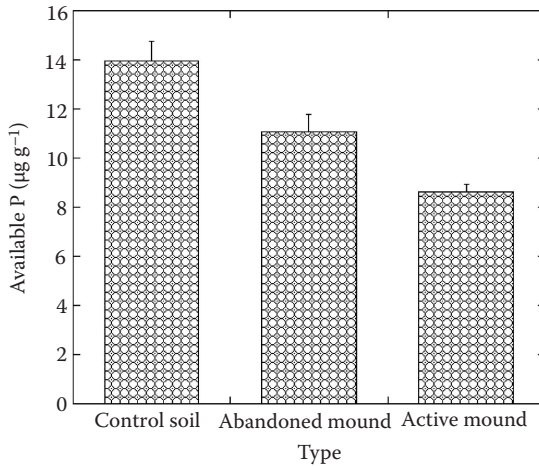


FIGURE 11.8 Extractable soil P concentrations for highly weathered soils (0–10 cm depth) from La Selva Biological Station in Costa Rica. Soils were collected from active *Atta cephalotes* ant mounds (Active mound), from mounds that were no longer active (Abandoned mound), and from soils adjacent to both active and abandoned mounds (Control soil). Data show that ant activity significantly reduced topsoil P availability and that this reduction lasts even after the mounds are abandoned. Because *Atta cephalotes* are believed to turnover all the soil of this forest on only a 200–300 year timescale (Perfecto and Vendermeer 1993), this activity could represent an important control over the P cycle.

11.4.3 NUTRIENT LIMITATION

In relatively static ecosystems, the traditional view of tropical nutrient limitation to ecosystem processes, such as net primary production (NPP) and soil respiration, suggests that younger less well-developed soils would be limited by N, and older soils limited by P. Looking at the results from a chronosequence in Hawaii, which maintains ecosystems where it is possible to vary a single state factor while holding the rest relatively constant (Vitousek 2004), the transition from N limitation of tree growth on young soils to N and P colimitation on intermediate-aged soils to P limitation on old soils is clear (Vitousek and Farrington 1997). An analogous assessment of soil C cycling along the same chronosequence suggested that soil microbial growth and respiration were more affected by N at the youngest site and P at the oldest site, in line with the results observed aboveground (Reed et al. 2011b). Thus, the scarcity of P in many lowland forests and the tendency toward N limitation in tropical montane systems that typically grow on less well-developed soil make sense (Tanner et al. 1998; Adamek et al. 2009). A number of cross-forest comparisons also suggest a positive relationship between soil P and tropical forest aboveground and belowground biomass, decomposition, soil respiration, and soil fauna (Wardle et al. 2004; Paoli et al. 2005; Espeleta and Clark 2007; McGlynn et al. 2007; Cleveland et al. 2011; Baribault et al. 2012), as do results from some fertilization studies where additions of P stimulate these and other lowland tropical forest ecosystem pools and fluxes (Cuevas and Medina 1988; Reed et al. 2007; Wieder et al. 2009;

Alvarez-Clare et al. 2013). And these patterns fit into the concepts of retrogression (Peltzer et al. 2010), where in the absence of large rejuvenating disturbances over timescales of thousands to millions of years, ecosystem properties such as NPP, decomposition, and nutrient cycling rates undergo substantial declines (Wardle et al. 2004; Paoli et al. 2005; Espeleta and Clark 2007; McGlynn et al. 2007; Cleveland et al. 2011; Baribault et al. 2012). Phosphorus is suggested as a strong factor in structuring tropical productivity, soil C cycling, and plant community composition. For example, a study conducted in a seasonally dry tropical forest in Panama assessed the responses of 550 tree species to eight environmental factors across a number of climatic and geological gradients (Condit et al. 2013). These results showed that soil P was one of the two strongest predictors of community composition, together affecting the distribution of more than half of the species.

However, while multiple lines of evidence suggest that soil P cycling has a role in regulating aspects of tropical ecosystem structure and function, particularly in lowland forests growing on highly weathered soil (Figure 11.9), a number of studies in tropical lowland forests suggest that there is much more complexity need for considerations of how P and other nutrients regulate ecosystem functions (Mirmanto et al. 1999; Newbery et al. 2002; Kaspari et al. 2008; Wright et al. 2011; Alvarez-Clare et al. 2013; Powers and Pérez-Aviles 2013; Turner et al. 2013b; Mayor et al. 2014; Turner and Wright 2014). In other words, nutrient limitation in tropical ecosystems is not as simple as wholesale limitation by P, and changes in the availability of different nutrients may elicit distinct responses. For example, an investment in the acquisition of a nutrient may be greater when that nutrient is limiting to growth. A fertilization study in Hawaii found that P additions consistently reduced phosphatase activity, mycorrhizal colonization, and P uptake capacity across sites. In contrast, excess N

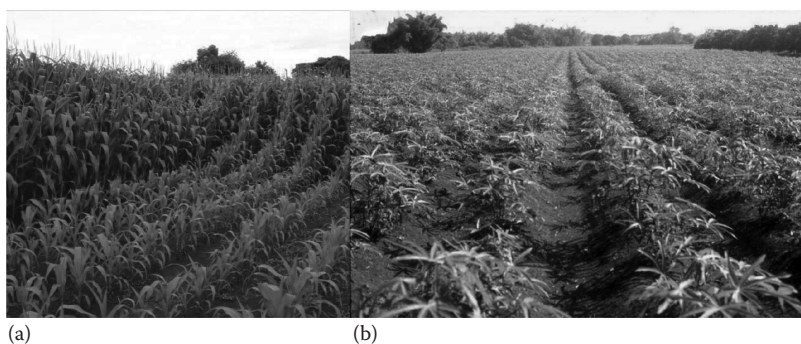


FIGURE 11.9 (See color insert.) Phosphorus availability on highly weathered soils can be a major constraint to agriculture in the tropics. (a) Adding P to nutrient-poor tropical soils can dramatically enhance crop production, and the picture shows the effects of P fertilization on plant growth in Brazil's cerrado. Maize plants in the background were fertilized with P, and they are much larger than the unfertilized maize plants in the foreground. (Courtesy of D.M.G. de Sousa.) (b) Some crops are much more commonly grown in the tropics than anywhere else on earth. Shown here is cassava farming in Nigeria where the International Institute for Tropical Agriculture. (Courtesy of Tunga Media, Niger State, Nigeria, <http://tungamediang.com>.)

was allocated to the construction of extracellular phosphatases to acquire P. Along these lines, a $^{32}\text{PO}_4$ fertilization experiment in wet tropical forest found that P fertilization saturated the soils, which overwhelmed biological P demand, thereby reducing biological controls. In contrast, N fertilization increased the available P through reduced P sorption to the soil surface (Olander and Vitousek 2004). A long-term fertilization study in Panama also found a significant decline in phosphatase activity in response to fertilization (Turner and Wright 2014). The increase in phosphatase production and reduced P sorption in response to N fertilization implies that even P-limited systems might increase productivity in response to increased N availability and highlights the complex effects of nutrient availability on ecosystem processes (Treseder and Vitousek 2001; Vitousek et al. 2010).

A fertilization experiment by Alvarez-Clare et al. (2013) further illustrates the complexity of nutrient limitation in tropical forested ecosystems. This study used a N \times P fertilization experiment in 30 \times 30 m plots in a lowland rain forest in Costa Rica to show that after nearly 3 years, at the community scale, the growth of smaller trees (5–10 cm diameter at breast height) was doubled in plots receiving P, and seedling survival increased from 59 to 78%, with no effects of N addition on any characteristics measured. But P had no effect on litterfall productivity, root growth, or growth of intermediate (10–30 cm) or large trees (>30 cm). The effect of P also varied by plant species: *Pentaclethra maculosa*, the most abundant species at the site, did not increase growth rates with fertilization, but *Socratea exorrhiza*, the most abundant palm, had more than two times higher stem growth rates with P additions. Thus, while the research suggests soil P availability is indeed a significant driver of plant processes, it also highlights the importance of considering different aspects of the plant community (e.g., size class and species identity) when considering an overall framework of nutrient limitation.

Another complexity when evaluating nutrient limitation in terrestrial ecosystems is the form and the quantity of fertilizer utilized (Sayer et al. 2012). For example, microbes produce enzymes according to economic rules, whereby the microbial enzyme production increases when complex nutrients are abundant and simple nutrients are scarce; however, this response is also mediated by the availability of C and N (Allison and Vitousek 2005). A large-scale litter manipulation experiment conducted in a wet tropical forest in Costa Rica found a significant positive effect of litter addition on leaf litter production 5 months after application. The magnitude of the effect was significantly positively correlated with the total P added in litter form (Wood et al. 2006); however, a similar long-term litter manipulation experiment in Panama found no effect of litter addition on forest productivity (Sayer et al. 2012). This study did, however, find a significant effect of litter addition on the concentration of organic P in the soil (Vincent et al. 2010). It is also possible that the volume of aboveground biomass added in response to P fertilization could depend upon the concentration and the timing of P application.

Micronutrients (e.g., molybdenum) in addition to N and P may also exert important controls on tropical forest ecosystems. A long-term fertilization experiment in a tropical forest in Panama has consistently found that micronutrients (B, Ca, Cu, Fe, Mg, Mn, Mo, S, Zn), as well as N and P, can exert varied effects on ecosystem pools and processes (Kaspari et al. 2008; Wright et al. 2011; Santiago et al. 2012; Turner

et al. 2013b; Mayor et al. 2014; Turner and Wright 2014; Wurzburger and Wright 2015). Although P was the only nutrient to increase soil microbial biomass or affect measured enzyme activities (Turner and Wright 2014), this fertilization study found no clear effect of P limitation on plant growth, root growth, or decomposition (Kaspary et al. 2008; Wright et al. 2011). This diversity of responses to P fertilization, both within and across tropical ecosystems, makes sense when considered in the context of multinutrient limitation (as well as limitation by other resources; Kaspary et al. 2008; Townsend et al. 2011) and reflects the heterogeneity of nutrient availability in soils across the biome and the tropics as a whole (Quesada et al. 2010; Cleveland et al. 2011). These results underscore that soil age alone is not sufficient to explain all the observed patterns in N versus P (or other nutrient) limitation and the importance of multiple processes for determining the balance of nutrient inputs, losses, and biological demand (Vitousek et al. 2010). Nevertheless, even with the advances made in our understanding of soil nutrient controls in tropical ecosystems over the last years, these results still represent a focus on only a handful of sites relative to the high within- and across-ecosystem diversities of the tropics. Clearly, more work is needed to understand how soil P and other nutrients help regulate the structure and the function of earth's tropical ecosystems. Finally, it is important to recognize that there are strong interactions among these nutrient cycles, such that P availability can affect N, for example, via N₂ fixation (Reed et al. 2011c; Wurzburger et al. 2012; Batterman et al. 2013; Reed et al. 2013; Nasto et al. 2014), and other nutrients can affect P (e.g., N stimulation of phosphatase activity; Marklein and Houlton 2012).

11.5 THE TEMPORALLY DYNAMIC NATURE OF TROPICAL PHOSPHORUS CYCLING ON HIGHLY WEATHERED SOIL

In addition to the high spatial heterogeneity of soil P, available soil P also exhibits a high temporal variation in tropical forested ecosystems, with the potential to substantially vary on timescales ranging from hours (Vandecar et al. 2011; Turner et al. 2003) to days (Wood et al. 2016) to months (McGrath et al. 2001). Temporal variation in biologically available P often correlates well with soil moisture availability, which can significantly fluctuate in tropical forested ecosystems, due to both short punctuated rainfall events and broad seasonal changes in rainfall (Singh et al. 1989; Lodge et al. 1994; Campo et al. 1998; McGrath et al. 2000; Wood and Lawrence 2008). These changes in soil moisture alter a suite of variables that are likely to affect the availability of P in tropical soils. For example, large rainfall events can drive abrupt spikes in soil moisture that stimulate rapid changes in soil chemistry (e.g., redox potential, pH, desorption of nutrients from minerals; Kieft 1987; Chacon et al. 2006; Liptzin et al. 2011; Vandecar et al. 2011; Hall et al. 2013; Wood et al. 2013), which, in turn, stimulates both microbial and plant activities (Kieft 1987; Singh et al. 1989; Tiessen et al. 1994; Cleveland et al. 2004). Decomposition rates are also correlated with soil moisture availability, and a large portion of available soil P is likely replenished via the decomposition of OM by microbes (Singh et al. 1989; Tiessen et al. 1994, Cleveland et al. 2013). Thus, increased soil moisture can result in P release via OM decomposition, and this P is made part of the available P pool. The time the P spends in the available pool depends upon immobilization, sorption, and leaching controls.

In addition to the effects of soil moisture availability, diurnal and seasonal changes in temperature can influence microbial decomposition rates, thereby releasing P bound in OM 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 uptake and growth, which would instead immobilize labile P, thereby reducing its availability in the soil as microbial activity increases (Lodge et al. 1994; Cleveland et al. 2004). Furthermore, environmental controls on above-ground processes, such as plant photosynthesis, can stimulate root activity (Tang et al. 2005; Vandecar et al. 2009; Yuste et al. 2010). This increase in root activity can draw down labile P in the soil to meet the demands of the plant processes (Vandecar et al. 2009). Furthermore, sites with higher root density may facilitate greater labile soil P uptake and increase competition for P with the microbial community (Pregitzer et al. 1998; Vandecar et al. 2009, 2011).

As a whole, which of these processes exert primary control on labile P in the soils is not well understood, and there is evidence that the dominant controls may substantially differ among tropical forest sites along varied timescales. In more humid tropical forests, available soil P tends to be higher in the wet season (Cleveland et al. 2002; McGrath et al. 2001; Turner et al. 2013b; Wood and Silver 2012). In contrast, dry tropical forest sites have observed higher available soil P during dry season months (Singh et al. 1989; Campo et al. 1998; Srivastava 1997). The timing of high soil P availability, regardless of the soil moisture content, tends to correspond with times when the microbial biomass is also high (Singh et al. 1989; Cleveland et al. 2004; Turner and Wright 2014). Many theories have been put forth to explain these patterns: Soil P availability may be higher during the dry season months in seasonally dry tropical forests because (1) the demand by the vegetation is low, (2) P is stored in microbial biomass and then released upon the rewetting of soils (Singh et al. 1989), and (3) there is reduced loss of P due to low leaching in the dry season months (Campo et al. 1998). In humid forest soils, higher P availability in the wet season has been hypothesized to be due to (1) reducing conditions in the soil that release Fe-bound P (Chacon et al. 2006), (2) cloudier skies during wet season months that lower plant demand for P and thus uptake (3) higher P mineralization rates in the wet season (Campo et al. 1998; Wood and Lawrence 2008).

This raises the question of why we observe opposite effects of moisture on P in wet versus dry forests. There is increasing evidence to suggest that prior conditions play an important role in determining the fate of P in soil. Soil incubation experiments have found that the addition of water to wet soils results in rapid immobilization of available soil P (Campo et al. 1998; DeLonge et al. 2013). In contrast, the addition of water to dry soils results in the immediate release of available P (via microbial turnover or mineralization; Campo et al. 1998; Turner and Haygarth 2001). The decomposer community could be contributing to observed changes; for example, fungi, microfungi, and bacteria vary in their response to moisture (Lodge 1993; Cornejo et al. 1994; Lodge et al. 1994). The periodicity and amplitude of redox oscillations could also play a role in determining the fate of P in tropical soils, with more stable conditions driving a decline in microbial diversity, changes in mineral reactivity, enzyme activity, as well as higher N losses from the soil system (DeAngelis et al. 2005; Pett-Ridge and Firestone 2005; Thompson et al. 2006; Hall and Silver 2013;

Hall et al. 2015). Taken together, these data suggest that P availability is varying on extremely fast timescales, and this dynamism has the potential to affect a myriad of aspects of tropical function and response to change.

11.6 TROPICAL SOIL PHOSPHORUS CYCLING AND GLOBAL CHANGE

Tropical forests exchange more CO₂ with the atmosphere than any other class of ecosystem (Foley et al. 2003; Beer et al. 2010), as well as accounting for over two-thirds of the earth's living terrestrial plant biomass (Pan et al. 2013) and representing nearly one-third of all soil C stocks (Jobbagy and Jackson 2000; Tarnocai et al. 2009). Given this expansive amount of C, investigations of tropical forest response to environmental drivers will be critical for our understanding of future climate and biogeochemical cycling at the global scale. Tropical ecosystems also house the majority of the world's population, which makes them exceptionally important when considering change in these systems, including at local, regional, and pantropical scales (Lewis et al. 2015). However, the vulnerability of tropical ecosystems to climate-related change is poorly understood and a topic of much debate (Lloyd and Farquhar 2000; Lewis et al. 2009; Clark et al. 2013; Cox et al. 2013; Good et al. 2013; Randerson 2013). At the same time, a limited ability to characterize tropical responses to global change may represent our largest challenge in appropriately predicting the future climate of our planet (Bonan and Levis 2010; Huntingford et al. 2013; Piao et al. 2013). It is in this context that nutrient cycling may be central to improving our understanding of and capacity to predict tropical ecosystem response to global change.

Human activities have significantly affected each of the soil-forming state factors, with large implications for soil development and function (Amundson and Jenny 1991). The tropics are predicted to experience striking increases in atmospheric CO₂ concentrations, unprecedented changes in temperature, considerable modifications to the amount and the timing of rainfall (Diffenbaugh and Scherer 2011; Mora et al. 2013), and significant changes to N and P deposition (Matson et al. 2002; Mahowald et al. 2005; Peñuelas et al. 2012; Peñuelas et al. 2013; Carnicer et al. 2015; Houlton and Morford 2015). Each of these anthropogenic perturbations has the potential to markedly affect tropical soil P cycling, which, as discussed earlier, could affect numerous aspects of tropical ecosystem structure and function. However, the manner in which an ecosystem's P cycle will respond to anthropogenic perturbation will depend upon both the nature of the perturbation and the characteristics of the soil.

Soil nutrient availability may be at the heart of determining how tropical ecosystems will respond to global change (Silver 1998a; Cernusak et al. 2013; Yang et al. 2014; Cavaleri et al. 2015; Reed et al. 2015). Increases in nutrient availability (e.g., via fertilization) consistently increase the productivity of terrestrial plants of both managed and unmanaged ecosystems (Sanchez and Buol 1975; Sanchez 1976; Elser et al. 2007; Vitousek et al. 2009). Soil nutrient availability has also been shown to positively affect the rates of soil CO₂ efflux and microbial biomass growth (Reed et al. 2011b; Wood and Silver 2012). Indeed, a synthesis of data from 92 forests in different climate zones underscored the crucial role nutrient availability plays in determining

net ecosystem productivity, suggesting that nutrient availability exerted a stronger control over the net ecosystem productivity than that of C input (i.e., gross primary production; Fernández-Martínez et al. 2014). This result conflicts with assumptions of nearly all global coupled C cycle–climate models, which assume that C inputs via photosynthesis are the dominant driver of biomass production and C sequestration. In addition, results from past free-air CO₂ enrichment (FACE) studies that explored plant and soil responses to increased CO₂ showed that nutrient limitation strongly constrained plant responses, and the data suggested that nutrient limitation became progressively more extreme over time for plants experiencing elevated CO₂ (Luo et al. 2004; Norby et al. 2010; Johnson 2006). But none of these CO₂ experiments occurred in tropical ecosystems, and none focused on P (but see Huang et al. 2014; Crous et al. 2015; Hoosbeek 2015; Norby et al. 2016). Due to the lack of a significant gaseous phase, the P cycle may be less able to respond to increased plant demand in the face of elevated CO₂ (Reed et al. 2015), which would mean that P regulation of C cycling responses to global change could become increasingly pronounced (Yang et al. 2014). A recent study comparing modeling, satellite, and FACE experimental data indeed suggests that CO₂ fertilization effects on plants are potentially much lower than what models would predict, and nutrient limitation was cited as a key reason for this response (Smith et al. 2015).

Our understanding of how warming and altered precipitation patterns will affect tropical forests via effects on soil P cycling is also quite poor (Silver 1998b; Wood et al. 2012; Meir et al. 2015). Nevertheless, kinetic controls dictate that changes in temperature could result in strong effects on decomposition and nutrient mineralization rates, as well as changes in soil weathering. Indeed, warming has been shown to increase nutrient mineralization rates in other biomes (Robinson et al. 1997), and increased mineralization could increase nutrient losses via leaching, thereby lowering nutrient availability and constraining C cycling over the longer term (Lodge et al. 1994). If warming initially increases and then drives down nutrient availability, processes such as microbial respiration and decomposition could become slow due to nutrient limitation (Hobbie and Vitousek 2000; Reed et al. 2011b). Reduced rainfall in tropical regions could significantly affect P cycling in tropical forest ecosystems. For example, experimental reduction of soil moisture in a wet tropical forest in Puerto Rico led to significantly reduced soil P availability, likely due to increased soil aeration and sorption of P to Fe oxides in the soil (Wood and Silver 2012). Changes in the patterns of rainfall could generate complex effects on soil P cycling. As discussed earlier, prior soil conditions matter, whereby the rewetting of dry soils compared with the wetting of soils that are already wet led to different fates of P in the soil. Furthermore, tropical microbes have the potential to adapt to preexposure to dry conditions (Bouskill et al. 2013), further adapting as wetting and drying cycles intensify (Evans and Wallenstein 2014).

In addition to CO₂ and climatic changes, human-induced changes to nutrient inputs, for example, N deposition, have the potential to both directly and indirectly affect tropical soil P cycling. These changes can stem not only from the differences in the absolute input of any single element (e.g., increased N or P deposition) but also from an imbalance in the relative proportions of these inputs (Peñuelas et al. 2012, 2013). However, our understanding of these effects and their controls remain notably

poor, and studies of coupled biogeochemical cycles in the context of change and stoichiometric perspectives offer an exciting line of tropical research.

As the human population continues to grow, the demand for agricultural productivity to meet the increasing demand for food and biofuel production will likely lead to the intensification of agricultural practices, particularly in tropical regions (Coomes et al. 2000; Tilman et al. 2002; Laurance et al. 2014; Smith et al. 2014; Lal 2015). Intensification of agriculture occurs in three ways: (1) expansion of the land area used, (2) increase in the frequency that a given area is used, and (3) intensification of the management controls (Trenbath et al. 1990). Changes to agricultural practices have been found to affect soil P availability. For example, changes to timing whereby the number of crop cycles are increased and the period the forest is allowed to recover (fallow) is reduced, has been found to reduce P availability in tropical soils (Arnason et al. 1982; Fujisaka 1991). These shorter fallow periods are thought to facilitate the loss of P from the system via soil mining and accelerated erosion (Fujisaka 1991; Mertz 2002) and could ultimately reduce the efficacy of this land management technique (e.g., Jakovac et al. 2015). In systems that utilize shifting agriculture, the timing of slashing and burning is also critical and also affects soil P cycling. Biomass is cut, left to dry, and burned just prior to the start of the wet season. The timing of slashing is important for allowing sufficient time for the biomass to dry, and the timing of burning is timed to minimize the loss of P in ash that can be blown off of the land surface and to maximize the plant growth and uptake of nutrients. In these agricultural systems, and many others, farmers rely on historical experience to determine the timing of slashing, burning, and planting (Ewel 1986). Changes in precipitation patterns could have significant effects on the efficacy of these practices as historical knowledge may no longer clearly inform land management decision-making. In addition to the intensification of cultivation practices, the increasing demand for agricultural lands has also led to the expansion of agriculture into areas previously considered lower quality.

Secondary forests (forests regenerating following land use conversion) in the tropics currently comprise more land area than that of their old growth counterparts. The legacy of land use drives profound changes in the community composition and the soil nutrient cycles of these secondary forests, and the trajectory of their recovery is influenced by P cycling. For example, Davidson et al. (2007) showed that after agricultural abandonment, secondary tropical forests on highly weathered soils may transition from N limitation near to the time of abandonment to P limitation as the forests reach later stages of succession. Over the course of succession, N became relatively more available and P relatively less available. Of course, this trajectory would be expected to differ depending on the type and the intensity of prior land use. For instance, the intensification of shifting cultivation currently occurring across the tropics was recently found to significantly reduce secondary forest resilience (Jakovac et al. 2015), which may be exacerbated by a slow recovery of P as land use intensifies.

11.7 CONCLUSIONS

Phosphorus availability is a critical component determining terrestrial ecosystem structure and function, particularly for ecosystems growing on highly weathered soils (i.e., Ultisols, Oxisols). Due to the effects of extensive weathering, these soils maintain unique soil P traits, and the specialized manner in which the soils cycle P has cascading effects on numerous aspects of the ecosystems themselves. For example, the availability of soil P has been linked with plant community composition, NPP, and a wide range of fundamental soil processes (e.g., OM decomposition, soil respiration, N₂ fixation, C, N, and P-related enzyme activity). Moreover, agriculture in the tropics is an increasingly important component of providing food for our growing human population, and effectively managing tropical soils in this context is at the heart of agricultural success. Even in unmanaged tropical ecosystems, due to the massive amounts of C, water, and energy exchanged between the tropical forest biosphere and the atmosphere, it is critical to understand the role P plays in determining the tropical responses to global change factors, such as increasing atmospheric CO₂ and climate change. Nevertheless, our understanding of tropical soil P cycling remains notably incomplete, particularly in the context of global change, although the implications of these multielement connections are large. As highlighted in this chapter, the scientific community has made great strides in our understanding of the P cycle on highly weathered tropical soils, but our ability to measure, scale, and forecast ecosystem functions in tropical ecosystems lags behind that of many other biomes. Further, the exceptional diversity and biogeochemical variation at multiple scales in the tropics complicates this task. Taken together, the data suggest that a soil perspective is a solid foundation on which to build an improved understanding of the tropical P cycle.

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