

Chapter 14

Phosphorus Cycling in Tropical Forests Growing on Highly Weathered Soils

Sasha C. Reed, Alan R. Townsend, Philip G. Taylor, and Cory C. Cleveland

14.1 Introduction

In 1976, Walker and Syers introduced a model describing patterns of soil phosphorus (P) pools and availability during ecosystem development (Fig. 14.1). The model suggested that, early in soil development, the majority of P is in primary mineral forms, mostly as apatite. As apatite is weathered, it releases biologically available forms of P (as PO_4^{3-}). Some P is taken up by plants and microbes and is ultimately returned to inorganic P (P_i) pools in the soil via mineralization, or remains within the soil in organic forms (P_o ; Fig. 14.1). However, during each turn of this cycle, some P may also be sorbed by secondary soil minerals, precipitated, or leached in organic or inorganic forms, slowly depleting the total and available P pools (Fig. 14.1).

The Walker and Syers (1976) model predicted that at intermediate levels of soil development, P would be fairly evenly distributed among different pools: primary mineral, secondary mineral, labile P, and soil P_o (Fig. 14.1). However, as soil development reaches more advanced stages, the total amount of P in the system would decline and much of the remaining P would be bound in insoluble or physically protected, nonlabile (i.e., not biologically available) forms. In contrast to carbon (C), nitrogen (N) and sulfur (S), P has no significant gaseous state [phosphane (PH_3) comprises a trivial portion of global P stocks (Toy 1973)], and the primary input of biologically available P is from mineral weathering or from atmospheric dust inputs (Chadwick et al. 1999). In essence, Walker and Syers

S.C. Reed (✉)

U.S. Geological Survey, Southwest Biological Science Center, Moab, UT 84532, USA
e-mail: screed@usgs.gov

A.R. Townsend and P.G. Taylor

Department of Ecology and Evolutionary Biology and the Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO 80303, USA

C.C. Cleveland

Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA

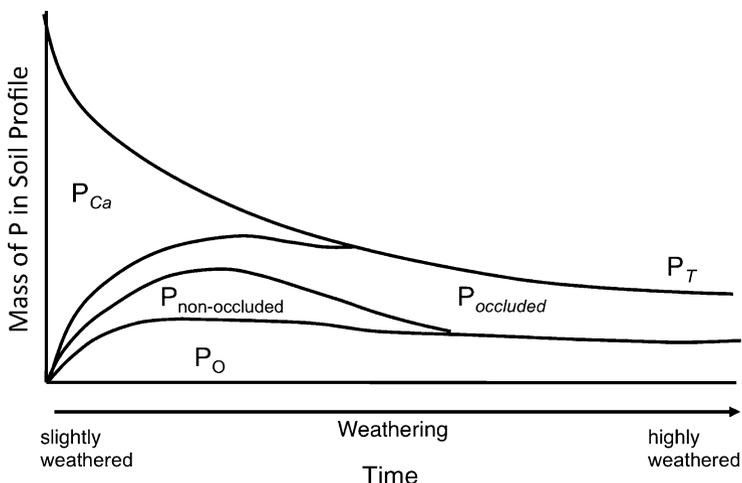


Fig. 14.1 Conceptual model modified from Walker and Syers (1976) showing variations in soil P pools during pedogenesis: P_T total soil P; P_{Ca} calcium phosphates; P_O organic matter P; $P_{occluded}$ sorbed P (relatively unavailable to organisms); $P_{nonoccluded}$ P in the soil solution (relatively available to organisms; often called “labile” P). The model suggests that the highly weathered soils (Ultisols and Oxisols) of many tropical forests 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

(1976) predicted that ecosystems on old, highly weathered soils would eventually reach a “terminal steady state” in which little P would remain available for biological uptake, ultimately leading to P limitation of ecosystem processes.

This model has been further tested and corroborated by multiple studies, including one that assessed nutrient availability and limitation using a fertilization study across a 4 million year substrate age gradient (Vitousek 2004). Results showed that soil P pools behaved as predicted by Walker and Syers (1976) over the ~4 million years of soil development (Crews et al. 1995), and that aboveground primary production was N-limited in the youngest soils (~300 years old), N and P colimited in the intermediate-aged soils (~20,000 years old) and limited by P alone in the oldest soils (~ 4.1×10^6 years old) (Fig. 14.2) (Vitousek and Farrington 1997; Harrington et al. 2001).

The US Department of Agriculture (USDA) soil classification system (Soil Survey Staff 2006) includes 12 distinct soil orders that are largely defined by the extent of soil weathering. While tropical forests contain all but one of the USDA soil orders (Gelisols; Palm et al. 2007), seven are common in tropical forests: Alfisols, Entisols, Inceptisols, Mollisols, Oxisols, Ultisols, and Vertisols (Table 14.1). The Alfisols and Mollisols represent two of the more fertile soils of the tropics, and contain relatively high quantities of mineral and available P (Table 14.1); these are the soils where much of the most productive tropical agriculture occurs (Sanchez 1976; Vitousek and Sanford 1986). In contrast, the Ultisols and Oxisols occupy the weathered end of the weathering spectrum and are

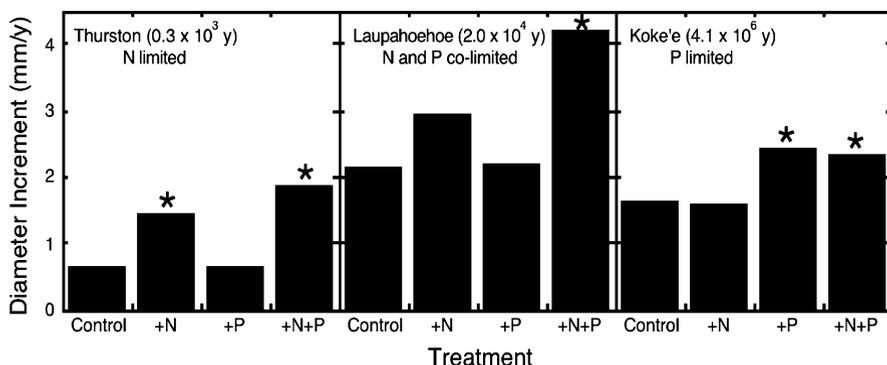


Fig. 14.2 Tree growth rates from a fertilization study along 4.1 million year substrate age gradient (modified from Vitousek and Farrington 1997). Bars show the means of tree growth (diameter increment) of *Metrosideros polymorpha* (the dominant tree species) for trees in control plots and in plots fertilized with N, P, and N + P. Within each site, treatment effects that were significantly different from the control are represented by asterisks. Data show that tree growth at the youngest site was N-limited, tree growth at the intermediate-aged site was colimited by N and P, and tree growth at the oldest site was P-limited

Table 14.1 Distribution of tropical forest soil orders (from Palm et al. 2007) and associated P pools

Soil order	Area (10 ⁶ ha)	Area (%)	Number (n) of samples tested	Labile P (μg/g)	Total organic P (P _o) (μg/g)	Total P (P _t) (μg/g)	P _o /P _t
Ultisol	654	27.0	7–8 ^a	33.3 ± 11.6	80.7 ± 19.6	203.6 ± 38.6	0.40
Oxisol	649	26.8	1–3 ^b	29.7 ± 4.5	152.0	321.3 ± 60.9	0.47
Inceptisol	416	17.2	5–9 ^c	71.4 ± 19.7	131.9 ± 20.2	753.6 ± 155.8	0.18
Entisol	244	10.1	2	17.5 ± 4.5	36.0 ± 11.0	684.5 ± 80.5	0.05
Alfisol	234	9.7	12	45.6 ± 9.6	83.8 ± 11.0	365.8 ± 101.5	0.23
Vertisol	71	2.9	3	43.3 ± 15.4	57.5 ± 12.5	529.3 ± 130.1	0.11
Mollisol	63	2.6	34–38 ^d	47.1 ± 4.4	109.1 ± 8.2	594.2 ± 101.9	0.18
Andisol	37	1.5	–	–	–	–	–
Aridisol	26	1.1	–	–	–	–	–
Histisol	26	1.1	–	–	–	–	–
Spodosol	5	0.2	–	–	–	–	–

Soil P concentrations – assessed using the Hedley-fractionation procedure (Tiessen and Moir 1993) – are provided for soil orders representing >2% of tropical forests and include soil-labile P (resin + bicarbonate-extractable inorganic and organic soil P), total organic P, and total P. The P concentrations represent global averages for each soil order. Soil P values are from Cross and Schlesinger (1995) and Johnson et al. (2003), using only data meeting the soil depth criterion used by Cross and Schlesinger (1995). P concentrations given are means ± s.e.m

^aLabile P and total organic P values were only available for seven of the eight Ultisols

^bTotal organic P values were only available for one of the three Oxisols

^cLabile P and total organic P values were only available for five of the nine Inceptisols

^dTotal organic P and total P values were only available for 34 of the 38 Mollisols

characterized by relatively low P availability (Table 14.1). Together these two soil orders are present in more than 50% of tropical forests (Table 14.1) (Vitousek and Sanford 1986; Palm et al. 2007).

Despite their P-poor status, Oxisols and Ultisols also contain some of the most productive forests on Earth. The warm temperatures and wet climate that combine to drive rapid soil development (Jenny 1941) also favor plant growth, and wet tropical forests account for ~35% of total global terrestrial net primary production (NPP) (Phillips et al. 1998; Grace et al. 2001) and store ~25% of the global terrestrial C found in biomass and soil (Schlesinger 1997; Jobbagy and Jackson 2000; Tarnocai et al. 2009). Understanding how P cycling regulates these large pools and fluxes of C is important at the global scale and, although climate and ecosystem models rarely explicitly consider the role of P in regulating C cycling (Parton et al. 2005; Thornton et al. 2009), there is growing evidence that P may strongly constrain the response of these extensive and productive tropical forests to anthropogenic change (e.g., Wardle et al. 2004; Cleveland and Townsend 2006; Paoli et al. 2008).

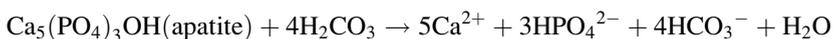
In the following sections, we describe P cycling in tropical forests, focusing on the most fundamental and unique aspects of the P cycle in forests growing on Ultisols and Oxisols, which are the dominant tropical soil orders (Table 14.1). We make only a few attempts to quantify pools and fluxes, per se, because data are rare and those that do exist suggest that the tropical P cycle is variable in both space and time (Townsend et al. 2008). Instead, we attempt to more generally describe the sources, internal transformations, and losses of P from tropical forests and to highlight the overall importance of P cycling for tropical forest function. In addition, we note that although Ultisols and Oxisols represent the most common tropical forest soil orders and are the focus of this analysis, tropical forests grow on many other soil types and the wide variation in tropical forest soil orders, species assemblages, and biogeochemical cycles results in a heterogeneous biome (Townsend et al. 2008).

14.2 The P Cycle in Tropical Soils

14.2.1 Tropical Soil P: Inputs

14.2.1.1 Parent Material

Of the six elements (C, hydrogen, N, oxygen, P, and S) that comprise 95% of the biosphere, P is somewhat unusual in that its biogeochemical cycle does not include a significant gaseous component (Toy 1973). Thus, as opposed to N that can be biologically “fixed” from the atmosphere, soil P must be supplied almost entirely from the weathering of underlying parent material (Schlesinger 1997) or from dust inputs (see Sect. 14.2.1.2). At early stages of ecosystem and soil development, the majority of P is in primary mineral forms (mostly as calcium apatite minerals) and, through time, weathering processes slowly dissolve the primary mineral P:



The rate of P weathering is variable and is dependent upon parent material, climate, and other drivers of soil development (Jenny 1941). Moreover, most rocks contain only small amounts of apatite, thus the weathering rate of P-containing minerals can ultimately constrain inputs of available P. In many temperate and high latitude terrestrial ecosystems, evidence suggests that when nutrients limit ecosystem processes, the limitation most commonly comes from N (Vitousek and Howarth 1991; Hooper and Johnson 1999) or from N and P together, not from P alone (see Elser et al. 2007; LeBauer and Treseder 2008). Nitrogen limitation has also been shown in tropical ecosystems where less weathered soils predominate (e.g., montane tropical systems) (Elser et al. 2007; LeBauer and Treseder 2008).

However, tropical forests are unique from many temperate or high latitude forests because they commonly exist on old, highly weathered substrates (Table 14.1). This is due to the high temperatures and rainfall that combine to promote rapid and extensive parent material weathering and because the long periods of intense weathering without large-scale disturbance have depleted much of the primary mineral P (in contrast to ecosystems that undergo episodic large-scale disturbances, e.g., glaciations, which effectively “reset” the soil development clock by exposing unweathered parent material at the surface). In the absence of such disturbances, most P in tropical forests resides in either organic forms (which vary in their availability) or in geochemically protected forms (i.e., P that is “sorbed” onto mineral surfaces or protected within mineral matrices) (occluded P; see Sect. 14.2.2.2). Thus, highly weathered tropical soils receive relatively small P inputs from parent material weathering (Walker and Syers 1976; Chadwick et al. 1999) and only small amounts of P reside in plant-available pools (Table 14.1) (Walker and Syers 1976; Cross and Schlesinger 1995; Johnson et al. 2003).

Although soil-available P is low in many lowland tropical forests, there is one important caveat to this general pattern: at the landscape scale, topographic variation can influence soil P cycling much like large-scale disturbances. For example, even in relatively well-developed soils on geomorphically unstable surfaces – such as slopes – high rates of soil erosion can rapidly expose parent material to weathering and effectively increase the parent material inputs of rock-derived nutrients (like P) (Vitousek et al. 2003; Bern et al. 2005). Thus, over relatively short timescales, P inputs and availability can be subsidized via erosion in forests with significant topographic relief. This does not contradict models of soil development (Jenny 1941; Walker and Syers 1976), but rather explains the significant spatial heterogeneity in soil P related to soil position (e.g., ridge top, slope).

In tropical forests, soils in geomorphically unstable sites can still be P-poor, but P may be high relative to sites occupying more stable surfaces (Silver et al. 1994; Chen et al. 1997; Vitousek et al. 2003). For example, when comparing the foliar element concentrations from soil on a flat, shield volcano in Hawai'i to those of an adjacent slope, Vitousek et al. (2003) used strontium isotopes to show that the parent material inputs of rock-derived elements (like P) on geomorphically unstable slopes could be twice the inputs on stable surfaces (13% vs. 6% of inputs from parent material, respectively).

14.2.1.2 Atmospheric Inputs

In the absence of substantial new inputs of rock-derived P from weathering, what are the dominant inputs of P to tropical forests? Evidence suggests that atmospheric inputs of P may be important in some tropical forests. For example, P can be transferred through the atmosphere over extremely long distances in the form of dust (Swap et al. 1992; Okin et al. 2004; Neff et al. 2006). The importance of dust inputs to tropical forest ecosystems depends on both the existing reservoir of P in the downwind ecosystem as well as on the total flux of dust being transported and deposited (Fig. 14.3). Multiple studies suggest that atmospheric P inputs to tropical forests may be critical for maintaining high NPP (Swap et al. 1992; Artaxo et al. 2002; Okin et al. 2004). For example, Chadwick et al. (1999) showed that, in sites in Hawai'i where rock-derived elements have been depleted, inputs of elements (like P) from dust may be necessary for sustaining NPP (Fig. 14.4). Thus, as soils weather and primary mineral P is depleted, atmospheric inputs may become the primary source of "new" soil P availability, and biological activity in highly weathered soils may increasingly rely upon atmospheric dust inputs (Fig. 14.4). This makes sense: in the absence of such external inputs, tropical ecosystems on

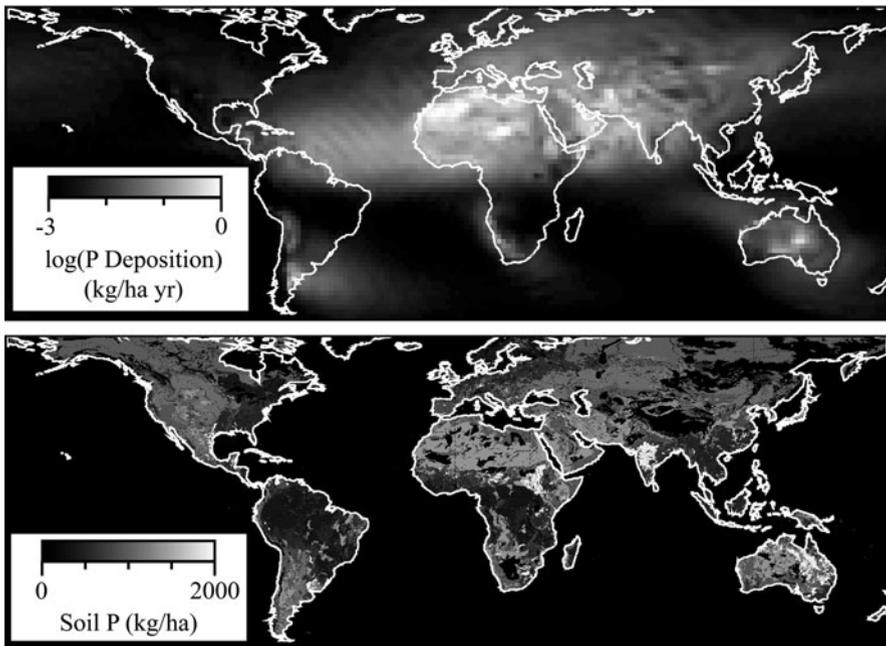


Fig. 14.3 Modeled estimates of global patterns in (a) P deposition from dust and (b) soil total P concentrations. Figure taken from Okin et al. (2004) and reproduced with the permission of the American Geophysical Union

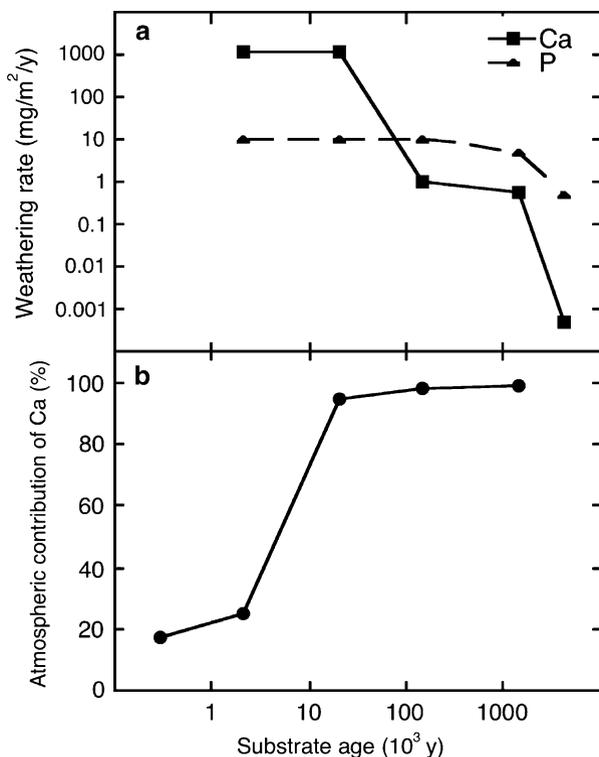


Fig. 14.4 Data from a 4.1 million year chronosequence in Hawai'i (Chadwick et al. 1999) showing (a) that rock-derived elements such as Ca and P are less likely to be released from parent material in older soils; and (b) an increased contribution of atmospheric inputs in supplying rock-derived elements. Ca and P values in a are calculated as the difference in mass of an element lost between two sites and the corresponding difference in age. In b, values represent the total percentage of soil Ca that was derived from the atmosphere, calculated by dividing the atmospheric contribution by the sum of atmospheric and weathering contribution. Figure reproduced from Chadwick et al. (1999) with the permission of the Nature Publishing Group

old, highly weathered soils would be predicted to reach a profound and irreversible state of P limitation (as predicted by Walker and Syers 1976).

Research also suggests that P from dust is important in mainland tropical forests (Fig. 14.3). For example, Swap et al. (1992) estimated that in the northeastern Amazon Basin, P inputs via dust range from 1 to 4 kg/ha per year, and they concluded that the high productivity of the Amazon rain forest is fueled, at least in part, by dust inputs originating in the Sahara/Sahel region in Africa. Similarly, Okin et al. (2004) suggested that Amazon Basin rain forests depend on aeolian deposition for the long-term maintenance of NPP.

The large fires now common in the Amazon Basin may also contribute significant amounts of P deposition, as P released from burning biomass may be

transferred (as particulates) through the atmosphere to unburned forests (Artaxo et al. 2002; Mahowald et al. 2005). For example, a study from four Amazonian forests suggested that the P requirements estimated for a year's worth of tropical rain forest growth (estimated as 0.6 g P/m^2 per year) could be provided by only 24 years of P deposition (Mahowald et al. 2005). However, data also suggest that these Amazon ecosystems may, on the whole, be experiencing net P losses to the atmosphere through processes such as biomass burning, anthropogenically induced losses of mineral aerosols, and biogenic particle movement (e.g., spores and pollen) (Mahowald et al. 2005).

Nevertheless, although atmospheric P inputs help maintain productivity, they may not be large enough to meet biological demand. For example, a study of six long-term chronosequences (in Alaska, Australia, Hawai'i, Sweden, and two sites in New Zealand) suggested that forests growing on highly weathered soils were in a "decline phase," as indicated by declines in NPP relative to younger sites (Wardle et al. 2004). Soil and foliar chemical data showed that these decline phases correlated with relatively high N:P ratios, suggesting that, in the absence of major disturbance, P constraints on NPP increase as forest ecosystems mature (Wardle et al. 2004). Moreover, this observation suggests that increases in P deposition in tropical forests (such as those resulting from increased land use and biomass burning) (Mahowald et al. 2005; Moulin and Chiapello 2006) could have positive effects on forest productivity.

14.2.2 Tropical Soil P: Internal Cycling and Transformations

14.2.2.1 Mineralization

Plant roots and soil microbes remove P from the soil solution, and use much of that P to build biomass. Subsequently, P is returned to the soil in organic forms as litterfall or dead plant or microbial biomass. Forest fauna are also a source of P_o to tropical soils, and faunal activity can affect P_o cycling in complex ways (Asawalam and Johnson 2007). In tropical forests growing on highly weathered soils, P_o represents a large proportion of total soil P (Ultisols and Oxisols contain ~44% organic P; Table 14.1), particularly when compared with other soil orders in which mineral P is the dominant form (all other soil orders contain ~17% organic P) (Cross and Schlesinger 1995). Large pools of aboveground biomass combined with low inputs of inorganic P from weathering make the return of plant biomass P to the forest floor the dominant input of P into tropical forest soils on an annual basis (Fig. 14.5) (e.g., Tiessen et al. 1984; Newberry et al. 1997). Thus, although P inputs via organic matter do not represent "new" P additions to the ecosystem per se, organic P recycling is a crucial mechanism for maintaining P stocks in tropical rain forests (e.g., Zou et al. 1992; Achat et al. 2009).

Organic P that enters the soil is a complex suite of compounds (e.g., nucleic acids and phospholipids) and variations in the overall chemistry, quantity, and

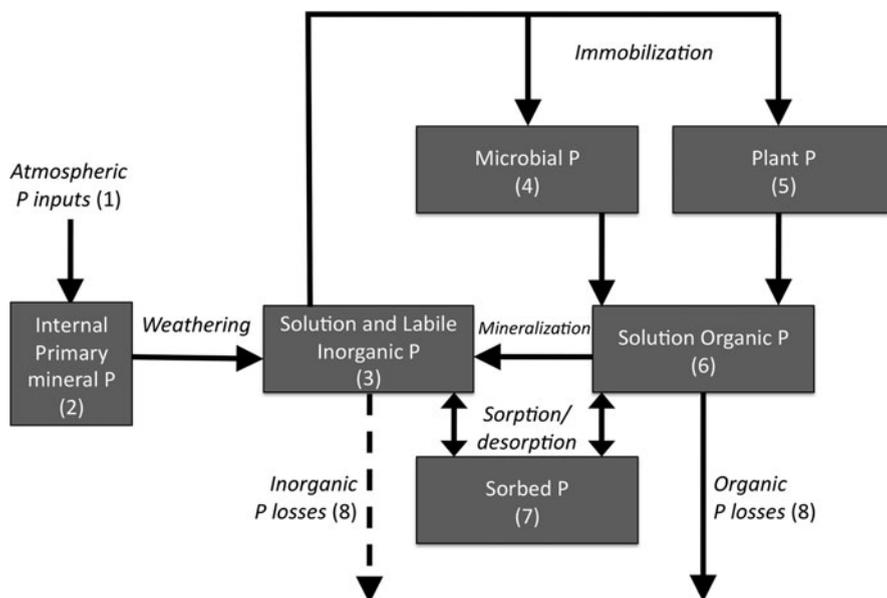


Fig. 14.5 Conceptual model of the terrestrial P cycle. *Boxes* represent the pools of P and *arrows* show the fluxes moving between pools. The size of the *boxes* and *arrows* do not represent pool size or flux rates. We highlight eight notable aspects of P cycling in tropical forests growing on weathered soils related to the pools and fluxes shown (1) Because available soil P pools are low in Ultisols and Oxisols, dust can represent a crucial input of P (see Sect. 14.2.1.2). (2) In contrast to other soil types, relatively low quantities of P are weathered from parent material into the soil matrix in highly weathered Ultisols and Oxisols (see Sect. 14.2.1.1). (3) Due to high rates of sorption (see Sect. 14.2.2.2) and large biological demand, soluble inorganic P pools in tropical forests are often relatively small. (4) Microbial P can comprise a large proportion of total P in tropical forests, and can play a crucial role in both desorbing P and maintaining P in biological cycles via storage within biomass (see Sects. 14.2 and 14.3). (5) Plants in tropical forests store a large amount of P, and tropical trees represent the dominant P source to soil. (6) Organic P represents a relatively large proportion of total soil P in tropical soils compared with many other soil types, and mineralization of P_o is an important biological P source (see Sect. 14.2.2.1). (7) Due to the physical and chemical properties of the clays dominating highly weathered soils, P sorption can effectively remove P from biologically available pools (see Sect. 14.2.2.2). (8) P can be lost from tropical soils in both organic and inorganic forms (see Sect. 14.2.4)

decomposability of organic P influence the chemistry and availability of the P_o pool (Anderson 1967; Condon et al. 1990). For example, organic P varies chemically depending on its source; both foliar and litter P content differ greatly among tropical forest tree species (Reich and Oleksyn 2004; Townsend et al. 2007) and thus the composition of the plant community influences the quantity, quality, and ultimate availability of P_o . Moreover, different plant biomass pools provide variable forms and quantities of P_o to soils. For instance, live leaves lost from trees (e.g., during a wind event) have nearly twice as much P per unit biomass than leaves that drop after senescence (McGroddy et al. 2004). Similarly, wood contains low

amounts of P relative to foliage, and wood C:P ratios are typically two to three orders of magnitude higher than C:P ratios of canopy leaves (Likens and Bormann 1995; McGroddy et al. 2004).

Variations in both the type and source of P_o entering the soil strongly influence its fate. For example, low quality litter (i.e., litter with high C:nutrient and/or lignin: nutrient ratios) often decomposes relatively slowly (Swift et al. 1979; Xuluc-Talosa et al. 2003; Wieder et al. 2009). Low quality litter can exacerbate low soil P availability via decreases in P_o mineralization rates and increases in P_o residence times (Vitousek 1982). In tropical forests, leaf litter C:P ratios are generally higher than in their temperate forest counterparts (McGroddy et al. 2004) because tropical trees growing on P-poor soil invest less P per unit biomass into their leaves (Fig. 14.6) (Townsend et al. 2007) and more efficiently retranslocate P from live tissue prior to leaf senescence (Vitousek 1984; Kitayama et al. 2000; McGroddy et al. 2004). In addition, microbes decomposing P-poor litter often immobilize P, and litter P concentrations have been shown to increase over the course of decomposition in tropical forests (Hobbie and Vitousek 2000; Cleveland et al. 2006).

Plants primarily take up P as orthophosphate molecules ($H_2PO_4^-$ and HPO_4^{2-}), which generally occur in tropical soil solutions at very low concentrations (Johnson et al. 2003). In order to increase the rate of transfer from P_o to P_i pools, the plants, their symbionts, and soil microbes may excrete phosphatase enzymes (see Nannipieri et al. 2011). Phosphatases represent a broad class of enzymes (e.g., acid and alkaline phosphomonoesterases) that catalyze the release of P_i by breaking phosphate ester bonds in organic molecules. The frequently observed increase in phosphatase activity in response to low P_i concentration by plants, bryophytes, mycorrhizae, and algae underscores the importance of this type of mineralization to the nutrition of living organisms (Kroehler and Linkins 1991; Duff et al. 1994; Whitton et al. 2005). In particular, data suggest that acid phosphatase activity may account for a significant proportion of plant and microbial P mineralization (and subsequent P uptake) (Kroehler and Linkins 1988; Moorhead et al. 1993). However, because both plants and microbes produce phosphatase enzymes and because roots and elevated microbial biomass often cooccur spatially (Tarafdar and Jungk 1987; Chen et al. 2002), the relative contribution of plants versus microbes to soil phosphatase enzyme production is difficult to discern.

Some data indicate that phosphatase activity is higher in weathered, P-poor soils relative to other soil types (Acosta-Martinez et al. 2007), though this is not always the case (Olander and Vitousek 2000; Treseder and Vitousek 2001). Nonetheless, fertilization studies performed in a variety of ecosystems suggest that phosphatase activity often decreases after P fertilization (e.g., McLachlan 1980; Caradus and Snaydon 1987; Allison and Vitousek 2005). These results make sense in the context of P-poor soils: if inorganic P is scarce but ultimately available in organic forms, then phosphatase production would provide a mechanism for increasing P availability. Alternatively, if P_i is readily available (e.g., after fertilization with P), then organisms may downregulate phosphatase enzyme production (Olander and Vitousek 2000; Houlton et al. 2008).

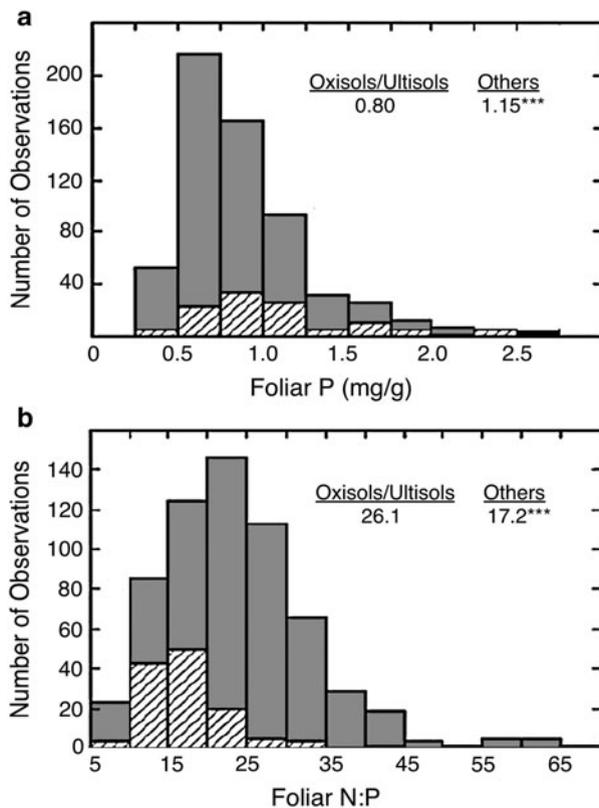


Fig. 14.6 Histograms of (a) foliar P and (b) N:P ratios (mass basis) from a tropical foliar database. Plants growing on Oxisols and Ultisols are shown in gray ($n = 462$) and those from other soil types are striped ($n = 110$). Values are means and asterisks denotes significant differences at $P < 0.001$. The data show that plants growing on highly weathered soils have lower foliar P concentrations and higher foliar N:P ratios compared with plants growing on other soils types. Figure taken from Townsend et al. (2007) and reproduced with the permission of the Ecological Society of America

More recently, the cloning of genes encoding extracellular phosphatases from plants (Haran et al. 2000; Wasaki et al. 2000; Miller et al. 2001) provides strong evidence for direct secretion and regulation of the expression of these genes in response to P limitation (see Wasaki and Maruyama 2011; George et al. 2011). Thus, P limitation may be “sensed” at the cellular level, driving modifications in gene expression by plants (and perhaps microbes) that result in increased phosphatase production. A recent model of plant P acquisition expands this idea by suggesting that different plant species could respond to competition for P_o by accessing discrete P_o pools (Turner 2008). Different species could produce phosphatase enzymes that target different organic P compounds. If so, plant-specific production of phosphatase enzymes could facilitate the coexistence of plant species

in diverse tropical forests growing on P-poor soil. Such a phenomenon has been observed for N in an arctic tundra community (McKane et al. 2002), but has not yet been examined in tropical forests.

A growing body of evidence also suggests strong linkages between N and P cycling in tropical forest soils, and phosphatases appear to be at the heart of this important interaction. As proteins, phosphatase enzyme production requires a significant investment of N, and N additions have been shown to enhance phosphatase activity (e.g., Zou et al. 1995; Treseder and Vitousek 2001). Consistent with that observation, it has been suggested that elevated foliar and litterfall N concentrations in N₂-fixing legumes may promote soil phosphatase production beneath these trees in tropical forests on weathered soil, thus increasing the ability of N-rich species to acquire P (e.g., Houlton et al. 2008). Although data to support this hypothesis are limited, this interaction offers another compelling explanation for the high abundance of symbiotic N₂-fixing species in tropical forests.

Interestingly, although N availability may fuel phosphatase production, one widely accepted model of organic matter mineralization suggests that P mineralization may be largely decoupled from the mineralization of C and N (McGill and Cole 1981). Whereas C and N are intricately bound in organic matter (Asner et al. 1997), P is bound by phosphate ester bonds that can be independently mineralized by phosphatase enzymes (McGill and Cole 1981). Thus, whether organisms mineralize organic substrates to obtain energy (in the form of reduced C) or N, both elements are mineralized, resulting in a relatively complex, coupled set of interactions involving biotic demand and enzyme production. In contrast, linkages between P limitation, phosphatase production, and P mineralization are more direct. Thus, P availability should be inversely related to phosphatase production, unless low availability of soluble organic P limits mineralization (organic P can be stabilized within the soil, thus it is not necessarily available for mineralization or leaching). McGill and Cole (1981) suggested a dichotomous system stabilizing and mobilizing C and N on the one hand, and P on the other. A decoupling of P mineralization from the mineralization of C and N may be particularly prevalent on highly weathered, P-poor soils.

Abiotic P mineralization is also possible via hydrolytic and photolytic reactions (Baldwin et al. 2003). Although photolytic mineralization rates may be relatively low at the forest floor (i.e., where there is little light), photolytic P mineralization reactions may play an important role in some tropical settings (e.g., forest treefall gaps). In addition, abiotic hydrolytic reactions could be important drivers of mineralization because soil water is often abundant in humid tropical forests. However, discriminating between abiotic and biotic hydrolytic reactions is difficult (Baldwin et al. 2003) and the role of abiotic processes in tropical forest mineralization remains poorly understood.

14.2.2.2 Sorption

The chemistry of weathered tropical soils affects nutrient mobility in somewhat unique ways. Mobility of nutrient ions in soil is a major factor controlling nutrient

cycling, because it affects the rate at which plant roots can extract nutrients and the rate at which nutrients are lost from the system. “Sorption” broadly describes any process that removes a reactant from a solution, thus reducing its mobility, and includes both adsorption and precipitation (Frossard et al. 1995). More specifically, P sorption refers to the removal of P from the soil solution into less reactive, geochemical sinks. In soils, both organic and inorganic forms of P are susceptible to sorption (e.g., Berg and Joern 2006), but the extent is influenced primarily by the concentration, chemistry, and solubility of soil P. Examples of sorption include P adsorption onto secondary clay minerals (e.g., kaolinite) or phosphate bound with iron (FePO_4) or aluminum (AlPO_4). Phosphorus sorption to soil particles occurs through different types of chemical bonds; for example, P sorption onto kaolinite occurs via a covalent bond between the oxygen of phosphate and the aluminum of the clay, whereas P precipitation into FePO_4 results from a bond between a phosphate oxygen and iron. Different sorption bonds vary in their stability and thus also in how readily the sorbed P can be desorbed.

Phosphorus sorption reactions are particularly important in highly weathered soils because strong soil sorption capacities compete with biological sinks for P, effectively reducing P availability (Uehara and Gillman 1980; Sollins et al. 1988). Intense weathering in Ultisols and Oxisols results in the prevalence of 1:1 clays (e.g., kaolinite) and in Al and Fe oxides and hydroxides that effectively sorb P (Sanchez 1976; Harrison 1987; Pant et al. 1994). As a result, sorbed inorganic P concentrations in many tropical soils often exceed those of soil solution P by several orders of magnitude (Sanchez 1976; Fig. 14.5), and fertilization studies have shown that, in highly weathered soils, P may be rapidly and nearly completely sorbed over short timescales (e.g., Sanchez 1976; Uehara and Gillman 1980; Oberson et al. 1997). Thus, the high P sorption capacity of tropical Ultisols and Oxisols can strongly influence the overall productivity of many forest and agricultural ecosystems in the tropics.

Whereas permanent negative charges are typical in the 2:1 clay-dominated soils common throughout the temperate zone, variable-charge clays are more common in highly weathered tropical soils (Sollins et al. 1988). In variable-charge clays, the electric charge results from protonation and deprotonation of surface hydroxyl groups (Gillman 1984; White and Zelazny 1986) and these hydroxyls occur at the edge of the 1:1 clays and Al and Fe hydroxides that dominate highly weathered soils. Because the charge of these clays varies with soil pH, small-scale changes in soil pH can affect the net soil charge and the mobility of both anions and cations (Sollins et al. 1988). Accordingly, the mobility of P in highly weathered soils will also vary with pH fluctuations, and P_i (PO_4^{3-}) 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 (Sollins et al. 1988). Decreased P mobility has implications for P limitation (see Sect. 14.3) and also for P losses through leaching (see Sect. 14.2.3).

Most previous research on soil P cycling has suggested that sorbed – or “occluded” forms of P – are relatively unavailable for biological uptake. However, a number of important questions remain about both the biological availability of

occluded P and the rate and controlling factors of occluded P return to available pools in tropical soils. Traditional definitions of occluded P suggest that it is unavailable and biologically inactive, at least over short timescales (Walker and Syers 1976; Wada 1985). Yet a growing body of evidence now indicates that occluded P may actually enter available pools on relatively short timescales, and movement from geochemical (i.e., sorbed) to available pools could be influenced by biological demand (Tiessen et al. 1984; Olander and Vitousek 2004; Richter et al. 2006). For example, data from a study of an aggrading forest on an Ultisol (Richter et al. 2006) suggested that traditional definitions of “labile,” “passive,” or “occluded” P may not be appropriate. Instead, Richter et al. (2006) showed that over 28 years of Piedmont forest regrowth on Ultisols, the increase in biological P came at the expense of the P residing in the Fe-, Al- and occluded-P pools, suggesting that plants may have access to these pools over decadal (or perhaps shorter) timescales.

Thus, the extent to which geochemical and biological sinks compete for soil P remains an ongoing area of research (Fig. 14.7b). For example, following P mineralization, P enters the soil solution before it is taken up by biota (Frossard et al. 1995), and in this way a high P sorption capacity could hinder the chance that high phosphatase activity will result in increased P availability. Yet, soil biota can increase the likelihood that mineralized P does not become geochemically immobilized via the secretion of low-molecular-weight-complexing molecules (such as organic acids) or by modifying the pH around them to promote solubilization and desorption of P. Similarly, some organisms have been shown to secrete organic acids to increase the solubility of organic P (Hayes et al. 2000; George et al. 2004), thus facilitating mineralization by increasing the solubility of the P_o substrate.

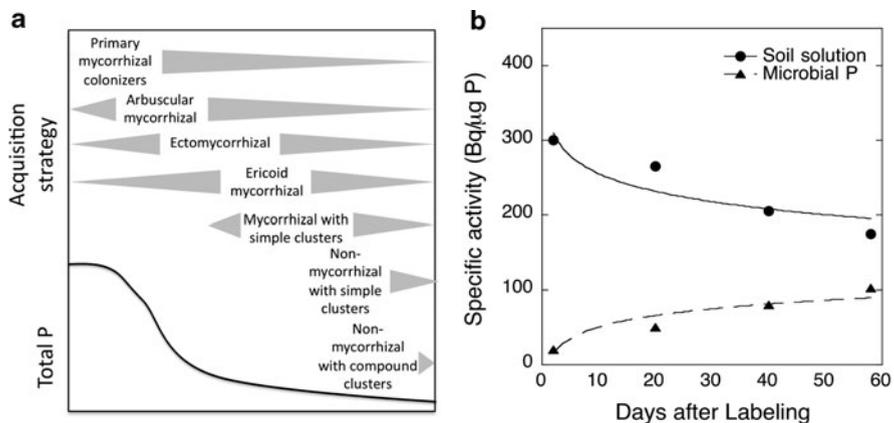


Fig. 14.7 Biological strategies for acquiring P. **(a)** Conceptual model showing changing plant nutrient-acquisition strategies with different levels of soil P. This panel was adapted from Lambers et al. (2008) with the permission of Elsevier. **(b)** The specific activities in the soil solution and in microbial biomass for an Alfisol soil after an initial radioisotope P addition. Data suggest that microbial organisms are able to effectively compete with geochemical sinks and rapidly uptake added radiolabeled P into their biomass. Figure recreated from Oehl et al. (2001) with the permission of Springer

More recent data also suggest that interactions between soil solution P and Fe oxides are more temporally dynamic than previously thought, and are strongly influenced by soil oxidation states (Baldwin and Mitchell 2000; Liptzin and Silver 2009). High biological activity and abundant rainfall in many tropical forests promote episodic anoxia (Silver et al. 1999; Schuur and Matson 2001), and corresponding fluctuations in redox potential can release Fe-bound P (Baldwin and Mitchell 2000; Liptzin and Silver 2009). This P can be subsequently resorbed or taken up by biota, and the sorption–desorption cycle of Fe and P bonding (in part determined by the soil and climate of tropical forests) helps regulate P cycling and availability.

Finally, whereas physical sorption reactions can remove P from the actively cycling pool, aggregate formation in soils dominated by weathered clays can also deplete the available P pool (Oades and Waters 1991; Denef et al. 2002; Six et al. 2002) by stabilizing P_o within aggregates (Merckx et al. 1985; Hassink 1997). Phosphorus may also diffuse from the outer surface of aggregates into the interior (Linguist et al. 1997), where P is physically protected from desorption (and biological uptake). Thus, the mineral soil aggregation found in many highly weathered soils (Oades and Waters 1991; Denef et al. 2002; Six et al. 2002) also contributes to low soil P availability.

14.2.3 Biological Responses to Low P Availability

Some data suggest that P availability limits ecosystem processes in tropical forests growing on highly weathered soil (see Sect. 14.3), yet the rates of many biological processes in this biome are among the highest on Earth (Raich and Schlesinger 1992; Cleveland et al. 1999; Gholz et al. 2000; Grace et al. 2001). Given this apparent contradiction, how do tropical forest organisms maintain high activity in the face of low P availability? A part of the answer lies in the fact that organisms in general – but especially in the tropics – have evolved a number of adaptations that effectively overcome low P availability. These strategies fall into two main categories: those that enhance P conservation and efficiency, and those that enhance P acquisition and uptake (Lajtha and Harrison 1995; Horst et al. 2001; Vance et al. 2003). Key conservation strategies include increased growth per unit P (high P-use efficiency), reallocation of internal P (e.g., foliar P resorption prior to leaf senescence), and modifications in metabolism to those that bypass P-requiring steps [e.g., alternative glycolytic reactions can bypass ATP-requiring steps under P starvation (Theodorou and Plaxton 1996; Schachtman et al. 1998; Raghothama 1999; Uhde-Stone et al. 2004)].

Plants growing on P-poor soils often have high P-use efficiencies, meaning that many tropical plants fix more C per unit P relative to those in other ecosystems (Vitousek 1984; Kitayama et al. 2000, 2004). One mechanism explaining the high P-use efficiency of tropical forest plants is that many show relatively high rates of P resorption from foliage prior to leaf senescence (Kitayama and Aiba 2002; Yuan

and Chen 2009). For example, foliar P resorbed from leaves of trees growing on soils with low P availability has been shown to be over 80% (Kitayama and Aiba 2002). Global comparisons suggest that foliar P resorption is highest in the lower latitudes of the tropics, with tropical foliar P resorption values ranging from 35 to 87% of foliar P (averaging 58%) compared with nontropical forests (ranging from 12 to 77% and averaging 47%) (Yuan and Chen 2009). In essence, P resorption provides an effective plant P recycling mechanism, short-circuiting the potential for losses of P during litter decomposition, and reducing plant P demand by conserving P within the plant.

Plants also have mechanisms for maximizing 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 organs involved in uptake. Accordingly, many plants counter low P availability through symbiotic relationships or a number of morphological adaptations that effectively increase root surface area, including mycorrhizal relationships that increase P transfer to roots (see Jansa et al. 2011) (Fig. 14.7a). Relative to temperate ecosystems, much less is known about the nature and importance of plant symbioses with mycorrhizal fungi, yet the data that do exist suggest that many tropical plants maintain symbiotic relationships with mycorrhizae (Janos 1980; Husband et al. 2002; Aldrich-Wolfe 2007). Similarly, plants often respond to low soil P availability by producing elongated root hairs (Fohse et al. 1991; Ma et al. 2001) or roots with unusual architecture (Al-Ghazi et al. 2003; Lopez-Bucio et al. 2005), both of which have been shown to increase plant access to soil P. For example, some tropical plants make use of lateral roots that scavenge P from the topsoil and litter layers (Herrera et al. 1978; Stark and Jordan 1978; Cuevas and Medina 1986) because these parts of the forest floor contain relatively high P concentrations.

Other plants also produce specialized root structures (e.g., proteoid roots or cluster roots) that allow plants to “mine” insoluble forms of inorganic P from the soil (Fig. 14.7a): cluster roots produce large amounts of carboxylates, which release P from strongly-sorbed forms (Lambers et al. 2008). Cluster-rooted plants have been observed in many tropical forests (Skene 1998), and many of the best-known cluster-rooted species are found in western Australia, an area with some of the most weathered and P-poor soils on Earth. Microbial organisms can also solubilize P from occluded inorganic pools, transforming it into available P. By releasing strong organic acids, certain bacteria can liberate P from inorganic P-bound molecules that are typically thought of as biologically inaccessible, and data suggest that organisms can effectively compete with geochemical sinks for soil P (Fig. 14.7b) (Olander and Vitousek 2004; Bünemann et al. 2004; Richter et al. 2006).

14.2.4 Tropical Soil P: Losses

Understanding controls over P losses from ecosystems is important because losses limit the accumulation of P pools at the ecosystem scale (Hedin et al. 2003). The

majority of P losses occur “out the bottom” as dissolved and/or particulate forms that are transported to streams via hydrologic flowpaths. Despite the high capacity for tropical soils to retain P, a combination of factors – hydrologic conditions, parent material age, soil properties, topography, and vegetative dynamics – can drive P loss from tropical forests. Across the tropics, riverine P concentrations tend to be relatively high in places where parent materials are P-rich, where there is rapid geologic uplift and/or erosion, or in relatively unweathered soils (Stallard and Edmond 1983; McDowell et al. 1995; Wilcke et al. 2001).

In tropical forests, water flow generally occurs via vertical infiltration and movement through soil profiles (Wilcke et al. 2001; Biggs et al. 2002). Despite their edaphic and topographic differences, surface water P outputs are dominated by groundwater sources of P in both lowland and montane tropical forests (Lewis et al. 1986; Markewitz et al. 2006). During times of low watershed discharge, P concentrations tend to be too high, which can result from the increased concentration of soluble P and/or increased interaction with the soil matrix (i.e., low rates of macropore flow). Some studies have shown a direct relationship between dissolved silicates and dissolved P (e.g., Hedin et al. 2003), suggesting that P is exported along with other weathered products as water dissolves silicate-based parent material in the soil profile. To date, however, it is unclear what forms of P occupy deep soil P reserves and how they may subsidize plant nutrient demand.

In lowland tropical forests on Oxisols and Ultisols, P concentrations are generally highest in surface soils and decline vertically through the soil profile because water carries mobile P through the hydrologic continuum from leaf litter leachate to stream flow. This probably reflects the strength of geophysical sequestration into refractory or occluded forms vertically through the soil profile, as well as the biological capacity for lowering P loss. Furthermore, compared with montane tropical forests (which are often underlain by less weathered soils and characterized by shorter soil hydrologic residence times), concentrations of dissolved inorganic and organic P in lowland tropical forests on more weathered soils are typically very low.

In some tropical regions, surface soil P pools can serve as export sources when soils permanently or temporarily saturate under rainfall events, and water flow direction shifts to lateral pathways through soil surface horizons. Consequently, the source of P export shifts to upper soil horizons where organically bound P can be horizontally transferred to aquatic systems (Saunders et al. 2006). Also, during periods of high rainfall a brief and rapid flushing of residual P pools can yield a positive relationship between stream discharge and dissolved P traveling via groundwater (Markewitz et al. 2006) and particulate P that probably originates from overland flow (Lewis et al. 1986).

In addition to the physical interactions that control P export, low P losses also reflect efficient biological P recycling in tropical plant–soil systems. Over the course of ecosystem development, Hedin et al. (2003) showed that the amount and stoichiometric composition of P loss changed in concert with ecosystem P status across a 4.1×10^6 year chronosequence. Shifts in ecosystem nutrient

status across the Hawai'i chronosequence determine, in part, the concentration of P loss. In forests where N availability limits plant growth, dissolved inorganic P concentrations in soil waters below the active rooting zones and in streams were on average fourfold higher (4–7 $\mu\text{g/L}$) than P-limited sites. For the older, P-limited forests growing on weathered soils, P concentrations were relatively low, particularly with respect to dissolved N losses.

Yet, among all sites on the chronosequence a positive relationship between silica and inorganic P was uniformly strong, most notably for sites severely limited by P. As mentioned above, this pattern points to a strong connection between hydrologic P losses and weathering among all soil types, even in the face of very low ecosystem P status. Moreover, organic forms of dissolved N and P were found to “leak” from all the sites along the chronosequence, essentially irrespective of ecosystem N or P status (Hedin et al. 2003). Persistent P loss despite high biotic P demand indicates that some P pools are somewhat insensitive to biological retention mechanisms. In pristine temperate systems in Chile, Hedin et al. (1995) found that such losses for the N cycle can constrain ecosystem-scale N accrual, which is a concept that remains largely untested for P in tropical systems.

At the watershed scale, the interactions between biological and hydrological dynamics are not well understood. Generally, hydrologic analyses of P export have focused on how runoff-generating processes (i.e., unsaturated and saturated overland or subsurface flow) control patterns of P loss. However, microbially mediated P transformations certainly play a large role in releasing P stabilized in geophysical and organic forms, yet the biological influence on P mobility at the watershed scale has been largely unexplored. Moreover, tropical land-use change via fire, conversion to pasture, deforestation, agriculture, and urbanization may alter both hydrological and biological controls over P loss from ecosystems.

Few studies have explored each of these disturbance processes, but P cycling and loss patterns are generally consistent with predictions from the successional theory of nutrient cycling and forest regrowth, where P loss and recycling become more conservative in converted landscapes (Vitousek and Reiners 1975; Bormann and Likens 1979). High biological P conservation may also stem from the depletion of available P pools enhanced by hydrologic P loss, or through a combination of high-temperature oxidation or removal of biomass. In old and highly weathered systems where P inputs are low and outputs are small, land conversion reduces P availability through biomass clearing or burning, as well as by driving available P into more recalcitrant pools (Markewitz et al. 2004). For example, in pastures and secondary forests near Paragominas, Brazil, bioavailable (Mehlich-III-extractable) P stocks have been reduced by ~ 1 kg/ha (despite P fertilization) compared to mature forests, presumably due to irreversible sorption to soil oxides (Markewitz et al. 2004). Also, increases in runoff volume and intensity associated with the removal of trees after land conversion can increase the export of particulate P via overland flow (Williams and Melack 1997; Neill et al. 2001).

14.3 Nutrient Limitation in Tropical Forests

While conceptual models suggesting declining P fertility with soil age have proven useful for understanding pedogenic processes across ecosystems (Fig. 14.1), they also have profound implications for understanding how P may regulate ecosystem processes in tropical forests. Specifically, tropical rain forest systems pose a unique set of problems related to nutrient cycling and limitation. In contrast to temperate systems in which N availability more commonly limits plant growth, decomposition, and organic matter storage, N appears to cycle in relative excess in many tropical ecosystems (e.g., Vitousek 1984; Matson and Vitousek 1990; Neill et al. 1995; Martinelli et al. 1999). The relatively N-rich status of tropical forests may result from the abundance of potentially N₂-fixing leguminous trees in the floras of tropical forests (Cleveland et al. 1999; ter Steege et al. 2006) and perhaps from high rates of free-living N₂ fixation occurring in soils and on leaf litter (Maheswaran and Gunatilleke 1990; Cleveland et al. 1999; Reed et al. 2008). Evidence suggesting relatively rich N economies in tropical forests also includes high rates of N cycling (Keller et al. 1986; Matson et al. 1987), high N trace-gas emissions (Hall and Matson 1999), and enriched foliar and soil ¹⁵N isotopic values, owing to increased fractionation rates in N-rich tropical systems and perhaps also high N₂ fixation inputs (Martinelli et al. 1999 and references therein). Thus, in contrast to many temperate forests, current evidence suggests that N may not limit ecosystem processes in many lowland tropical forests on highly weathered soils.

Although direct tests of P limitation in tropical forests have been rare, indirect attempts to assess limitation suggest P constraints to multiple ecosystem processes. For example, Vitousek (1984) investigated patterns of N, P, and calcium (Ca) cycling in litterfall, and found that lowland tropical forests had more N and lower dry litter mass:N ratios than temperate forests. Similarly, Ca return to soil via leaf litter was high in tropical forests. However, Vitousek (1984) found that tropical forests had very low rates of P return and notably high dry litter mass:P ratios relative to temperate forests, suggesting an efficient P cycle characteristic of a P-limited system (Vitousek 1984; Vitousek and Sanford 1986). Data from soil chronosequences (Walker and Syers 1976; Vitousek and Farrington 1997; Wardle et al. 2004) also suggest that P limitation increases with time, as soil P availability declines and foliar N:P ratios and P resorption rates increase over the course of soil development. Thus, soils at the weathered end of the pedogenesis spectrum (like Ultisols and Oxisols) may be sufficiently depleted in P that P limits ecosystem processes.

Although uncommon, direct nutrient manipulations of nutrient fertility in tropical forests on weathered soil also suggest P constraints on ecosystem processes. In Hawai'i, long-term fertilizations with both N and P showed that primary production on old tropical soils was clearly P-limited (Fig. 14.2) (Vitousek and Farrington 1997). Fertilization with P at this older site elicited increases in stand-level wood increment, leaf area index (LAI), and aboveground NPP (Herbert and Fownes 1995; Vitousek and Farrington 1997; Harrington et al. 2001). Similarly, root ingrowth

studies following fertilization in a tropical forest site on an Oxisol soil in the northern Amazon Basin suggested that fine root growth was strongly constrained by P (and perhaps Ca) availability (Cuevas and Medina 1988). In contrast, fertilizer additions to a forest on a young Inceptisol soil in the mountains of western Venezuela revealed that litterfall mass responded more positively to N than P additions (Tanner et al. 1992), and similar tree growth responses were observed on young soil types undergoing fertilization with N and P in Hawai'i (Vitousek and Farrington 1997). Thus, although caution must be used when making broad generalizations to describe nutrient limitation in tropical ecosystems as a whole, there is some evidence indicating that low P availability may limit primary production on the highly weathered soils (Ultisols and Oxisols) common throughout the humid tropics.

Data also suggest that microbial processes in tropical rain forests may be limited by soil P availability. For example, a field experiment in a tropical rain forest in Costa Rica showed that soil respiration increased by nearly 40% in soils fertilized with mineral P for 2 years (Fig. 14.8a) (Cleveland and Townsend 2006). These data are noteworthy given that the P-induced increase in soil CO₂ flux was ~60% of the size of the total soil C flux from mid- to high-latitude forests. This increase in soil CO₂ efflux was not related to an increase in litter mass loss rates (Cleveland et al. 2006), but instead data suggested that P fertilization resulted in the heterotrophic mineralization of a larger proportion of the organic C moving from the litter layer into soil (Cleveland and Townsend 2006). Another study at this site suggested that the P content of leaf litter strongly regulated its decomposition rate (Fig. 14.8b) (Wieder et al. 2009), suggesting that both the rate of organic matter release from the litter layer and C efflux to the atmosphere are limited by P availability.

Aspects of the tropical forest N cycle are also affected by P availability. For example, P fertilization has been shown to increase atmospheric N₂ fixation rates in tropical forest epiphytes (Benner et al. 2007), leaf litter, and soil (Fig. 14.8c) (Reed

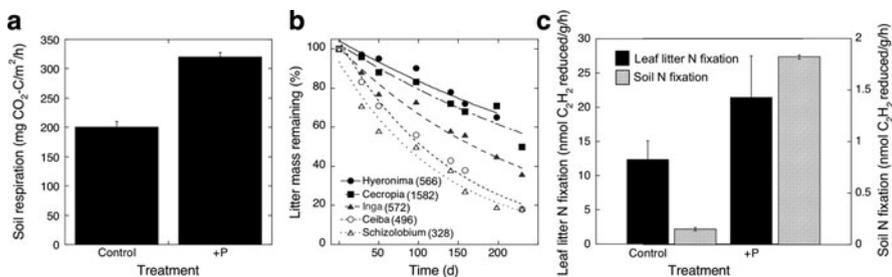


Fig. 14.8 Phosphorus limitation to microbial processes in a Costa Rica tropical rain forest. Data show that (a) field soil respiration is increased by P fertilization, (b) leaves from species with higher relative P concentrations (e.g., lower C:P ratios) decompose more rapidly on the forest floor, and (c) leaf litter and soil free-living N₂ fixation are stimulated by P additions. Leaf C:P ratios in b are given in parentheses following the plant genus. Data are taken from (a) Cleveland and Townsend (2006); (b) Wieder et al. (2009); recreated with the permission of Springer; and (c) Reed et al. (2007)

et al. 2007). Furthermore, an investigation of symbiotic N₂ fixation across a P gradient in Hawai'i showed that soil P availability and legume nodule N₂ fixation rates were positively related (Pearson and Vitousek 2002). In addition, data suggest that natural, species-specific variation in foliar P concentrations (Townsend et al. 2007) regulate free-living N₂ fixation rates in the canopy as well as on the forest floor, with higher P concentrations correlating with higher free-living N₂ fixation rates (Reed et al. 2008). Phosphorus limitation of free-living N₂ fixation rates is noteworthy given recent research suggesting that tropical forest legumes may not be fixing large amounts of N₂ (e.g., Gehring et al. 2005). Thus, P may directly regulate N inputs into tropical rain forests via limitation to N₂ fixation.

The observation that P limits microbial activity in tropical forests on highly weathered soils (Fig. 14.8) has a number of implications for nutrient cycling, some of which may seem contradictory, and which operate at a variety of timescales. For example, if microbial immobilization of P is high, it could accentuate P constraints on plant growth. However, microbes may ultimately represent a crucial biological valve for P that prevents more permanent losses (see Sect. 14.2.4). In tropical forest ecosystems, the microbial P pool represents an important component of the soil organic P pool (Paul and Clark 1989; Bünemann et al. 2004), and microbial "storage" of P in tropical soils may prevent the movement of soil P into unavailable pools and/or leaching losses. Thus, microbial activity could act to limit more severe P limitation as soils age.

14.4 Global Change and Soil P in the Tropics

Both climate and land-use changes, among others, are affecting tropical forests (e.g., Clark 2004; Asner et al. 2005; Malhi et al. 2009; Friedlingstein et al. 2010), and the P cycle could strongly mediate tropical ecosystem responses to these perturbations (Fig. 14.8) (Vitousek and Farrington 1997; Cleveland and Townsend 2006). For example, multiple studies suggest that intact tropical forests may be acting as significant sinks for atmospheric CO₂ (Stephens et al. 2007; Phillips et al. 2008; Lewis et al. 2009). However, P limitation has the potential to strongly constrain this response both directly (via limitation to NPP) (Vitousek and Farrington 1997) and indirectly (via P regulation over the availability of other nutrients such as N) (Reed et al. 2007). For example, if increased atmospheric CO₂ concentrations stimulate tree growth, ecological stoichiometry suggests that this will drive higher plant nutrient (including P) demand. This could result in increases in organic P in live biomass and decaying organic matter. If such increases come at the expense of lower soil P availability in these already P-poor soils, increasing litter C:P ratios could provide a negative feedback by suppressing decomposition rates (Vitousek 1982). In this way, soil P cycling could strongly regulate forest responses to global change, and these controls will probably be dynamic over multiple timescales. Accordingly, accurate predictions of the future tropical C balance require a more

robust incorporation of P cycling, a component of biogeochemical cycling almost wholly absent from ecosystem-scale C cycling models (Parton et al. 2005).

In addition, tropical land use change via fire, forest conversion to pasture, deforestation, agriculture, and urbanization will certainly alter P cycling in tropical ecosystems, and multiple lines of evidence suggest that such perturbations may enhance P losses and exacerbate P limitation. For example, Ultisol soils in Costa Rica showed large losses of P_i and organic matter after conversion from forest to pasture (P_i was reduced from 7.6 ± 0.5 to 4.7 ± 0.6) (Cleveland et al. 2003), and data suggest a postperturbation transition from biologically dominated P cycling to a cycle dominated by geochemical processes (McGrath et al. 2001). What this transition could mean for tropical productivity remains unknown.

Furthermore, many previously deforested tropical landscapes are now recovering from conversion to pasture, and these successional forests occupy an increasingly large proportion of the total tropical forest area. The legacy of land conversion and management has driven profound changes in soil nutrient cycles of these secondary forests, and the trajectory of their recovery will undoubtedly be influenced by P cycling. For example, Davidson et al. (2007) studied two forest chronosequences (using secondary forests that ranged in age from 3 to 70 years and two mature forests) to show that, after agricultural abandonment, secondary forests on highly weathered soils initially showed signs of N limitation. However, over the course of succession, N became relatively more available and P relatively less available, suggesting a transition from N limitation to P limitation during secondary forest succession.

Finally, increased socio-economic demand for agricultural products is driving accelerating rates of deforestation in the tropics and increased expansion of intensive agriculture. For example, soybean production on nutrient-poor soils in Brazil has increased dramatically in the last decade, and requires high P inputs to sustain high crop productivity. Given some of the unique and important roles of P in the biogeochemistry of tropical soils, research on the effects of such activities on P cycling in these emerging ecosystems is crucial (e.g., Sanchez et al. 1982; Oberson et al. 2001) because our understanding of P cycling (and its coupling with other biogeochemical cycles) in active and recovering agricultural Oxisols and Ultisols remains poor. Taken together, data suggest that global change could strongly affect P cycling in tropical landscapes and that these effects could feedback to regulate ecosystem responses to global change.

14.5 Conclusions

Phosphorus availability is crucial to the functioning of all ecosystems, yet could be especially so for tropical forests where P availability appears to limit multiple ecosystem processes. In light of the fact that tropical forests exchange more C with the atmosphere than any other biome and store 25% of global terrestrial C, an enhanced understanding of how P regulates tropical ecosystem function may be

disproportionately important for forecasting future climate. Despite significant advances in recent years, we suggest that there is an on-going need for research to be carried out in the following areas to improve our understanding of P cycling in tropical ecosystems:

1. Exploration and quantification of the coupling between the P cycle and the cycles of C and N. In particular, more direct assessments of P limitation to NPP are needed.
2. Understanding of the chemical diversity, turnover, and availability of soil organic P in tropical systems. Organic P represents the largest stocks and losses of P from terrestrial tropical ecosystems, yet we know relatively little about the chemical composition of this important pool.
3. Potential interacting impacts of changing climate, land use, and biogeochemical cycles on P pools and fluxes for tropical rain forests, and the attendant feedbacks to global change.
4. Consideration of how we define and measure “available” or “occluded” P pools. What pools are accessible by what organisms on what timescales?

Acknowledgments Projects supported by the National Science Foundation’s Division of Environmental Biology and the Andrew Mellon Foundation contributed to the thoughts and ideas discussed in this chapter. We are grateful to Astrid Oberson and an anonymous reviewer for their insightful suggestions and to Natalie Mahowald and Gregory Okin for providing a high resolution version of Figure 14.3.

References

- Achat DL, Bakker MR, Augusto L, Saur E, Sousseron L, Morel C (2009) Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods. *Biogeochemistry* 92:183–200
- Acosta-Martinez V, Cruz L, Sotomayor-Ramirez D, Perez-Alegria L (2007) Enzyme activities as affected by soil properties and land use in a tropical watershed. *Appl Soil Ecol* 35:35–45
- Aldrich-Wolfe L (2007) Distinct mycorrhizal communities on new and established hosts in a transitional tropical plant community. *Ecology* 88:559–566
- Al-Ghazi Y, Muller B, Pinloche S, Tranbarger T, Nacry P, Rossignol M, Tardieu F, Doumas P (2003) Temporal responses of *Arabidopsis* root architecture to phosphate starvation: evidence for the involvement of auxin signaling. *Plant Cell Environ* 26:1053–1066
- Allison S, Vitousek P (2005) Responses of extracellular enzymes to simple and complex nutrient inputs. *Soil Biol Biochem* 37:937–944
- Anderson G (1967) Nucleic acids, derivatives and organic phosphates. In: McLaren A, Peterson G (eds) *Soil biochemistry*, vol 1. Marcel Dekker, New York, NY
- Artaxo P, Martins J, Yamasoe M, Procopio A, Pauliquevis T, Andreae M, Guyon P, Gatti L, Leal A (2002) Physical and chemical properties of aerosols in the wet and dry seasons in Rondonia, Amazonia. *J Geophys Res* 107:D20
- Asawalam DO, Johnson S (2007) Physical and chemical characteristics of soils modified by earthworms and termites. *Commun Soil Sci Plant Anal* 38:513–521
- Asner GP, Seastedt TR, Townsend AR (1997) The decoupling of terrestrial carbon and nitrogen cycles. *Bioscience* 47:226–234

- Asner GP, Knapp DE, Broadbent EN, Oliveira PJC, Keller M, Silva JN (2005) Selective logging in the Brazilian Amazon. *Science* 310:480–482
- Baldwin D, Mitchell A (2000) The effects of drying and re-flooding on the sediment and soil nutrient and river-floodplain systems: a synthesis. *Regul River* 16:457–467
- Baldwin D, Howitt J, Beattie J (2003) Abiotic degradation of organic phosphorus compounds in the environment. In: Turner B, Frossard E, Baldwin D (eds) *Organic phosphorus in the environment*. CABI, Wallingford, UK
- Barber S (1984) *Soil nutrient bioavailability*. Wiley, New York, NY
- Benner JW, Conroy S, Lunch CK, Toyoda N, Vitousek PM (2007) Phosphorus fertilization increases the abundance and nitrogenase activity of the cyanolichen *Pseudocyphellaria crocata* in Hawaiian montane forests. *Biotropica* 39:400–405
- Berg AS, Joern BC (2006) Sorption dynamics of organic and inorganic phosphorus compounds in soil. *J Environ Qual* 35:1855–1862
- Bern CR, Townsend AR, Farmer GL (2005) Unexpected dominance of parent-material strontium in a tropical forest on highly weathered soils. *Ecology* 86:626–632
- Biggs TW, Dunne T, Domingues TF, Martinelli LA (2002) Relative influence of natural watershed properties and human disturbance on stream solute concentrations in the southwestern Brazilian Amazon Basin. *Water Resour Res* 38:1150
- Bormann F, Likens G (1979) Catastrophic disturbance and the steady-state in northern hardwood forests. *Am Sci* 67:660–669
- Bünemann E, Smithson PC, Jama B, Frossard E, Oberson A (2004) Maize productivity and nutrient dynamics in maize-fallow rotations in western Kenya. *Plant Soil* 264:195–208
- Caradus J, Snaydon R (1987) Aspects of the phosphorus nutrition of white clover populations. II. Root exocellular acid phosphatase activity. *J Plant Nutr* 10:287–301
- Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. *Nature* 397:491–497
- Chen Z, Hsieh C, Jian F, Hsieh T, Sun I (1997) Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. *Plant Ecol* 132:229–241
- Chen C, Condon L, Davis M, Sherlock R (2002) Phosphorus dynamics in the rhizosphere of perennial ryegrass (*Lolium perenne* L.) and radiata pine (*Pinus radiata* D. Don.). *Soil Biol Biochem* 34:487–499
- Clark DA (2004) Tropical forests and global warming: slowing it down or speeding it up? *Front Ecol Environ* 2:73–80
- Cleveland CC, Townsend AR (2006) Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proc Natl Acad of Sci USA* 103:10316–10321
- Cleveland CC, Townsend AR, Schimel DS, Fisher H, Howarth RW, Hedin LO, Perakis SS, Latty EF, Von Fischer JC, Elseroad A, Wasson MF (1999) Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems. *Global Biogeochem Cycles* 13:623–645
- Cleveland CC, Townsend AR, Schmidt SK, Constance BC (2003) Soil microbial dynamics and biogeochemistry in tropical forests and pastures, southwestern Costa Rica. *Ecol Appl* 13:314–326
- Cleveland CC, Reed SC, Townsend AR (2006) Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology* 87:492–503
- Condon L, Moir J, Tiessen H, Stewart J (1990) Critical evaluation of methods for determining total organic phosphorus in tropical soils. *Soil Sci Soc Am J* 54:126–1266
- Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions an ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76:1407–1424
- Cross AF, Schlesinger WH (1995) A literature review and evaluation of the Hedley fractionation: applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. *Geoderma* 64:197–214

- Cuevas E, Medina E (1986) Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia* 68:466–472
- Cuevas E, Medina E (1988) Nutrient dynamics with Amazonian forests. *Oecologia* 76:222–235
- Davidson EA, de Carvalho C, Figueira A, Ishida F, Ometto J, Nardoto G, Saba R, Hayashi S, Leal E, Vieira I, Martinelli L (2007) Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447:995–999
- Denef K, Six J, Merckx R, Paustian K (2002) Short-term effects of biological and physical forces on aggregate formation in soils with different clay mineralogy. *Plant Soil* 246:185–200
- Duff S, Sarath G, Plaxton W (1994) The role of acid-phosphatases in plant phosphorus metabolism. *Physiol Plant* 90:791–800
- Elser J, Bracken M, Cleland E, Gruner D, Harpole W, Hillebrand H, Ngai J, Seabloom E, Shurin J, Smith J (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10:1135–1142
- Fohse D, Claassen N, Jungk A (1991) Phosphorus efficiency of plants II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species. *Plant Soil* 132:261–272
- Friedlingstein P, Cadule P, Piao SL, Ciais P, Sitch S (2010) The African contribution to the global climate-carbon cycle feedback of the 21st century. *Biogeosciences* 7:513–519
- Frossard E, Brossard M, Hedley M, Metherell A (1995) Reactions controlling the cycling of P in soils. In: Tiessen H (ed) *Phosphorus in the global environment*. Wiley, Chichester, UK
- Gehring C, Vlek PL, Souza LA, Denich M (2005) Biological nitrogen fixation in secondary regrowth and mature rainforest of central Amazonia. *Agric Ecosyst Environ* 111:237–252
- George T, Richardson A, Hadobas P, Simpson R (2004) Characterization of transgenic *Trifolium subterraneum* L. which expresses phyA and releases extracellular phytase: growth and P nutrition in laboratory media and soil. *Plant Cell Environ* 27:1351–1361
- George TS, Fransson A-M, Hammond JP, White PJ (2011) Phosphorus nutrition: rhizosphere processes, plant response and adaptations. In: Bünemann E, Oberson A, Frossard E (eds) *Phosphorus in action: biological processes in soil phosphorus cycling*. Soil biology, vol 26. Springer, Heidelberg. doi: [10.1007/978-3-642-15271-9_10](https://doi.org/10.1007/978-3-642-15271-9_10)
- Gholz H, Wedin D, Smitherman S, Harmon M, Parton W (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Glob Change Biol* 6:751–765
- Gillman G (1984) Using variable charge characteristics to understand the exchangeable cation status of oxic soils. *Aust J Agric Res* 22:71–80
- Grace J, Malhi Y, Higuchi N, Meir P (2001) Productivity of tropical rain forests. In: Roy J, Saugier B, Mooney H (eds) *Terrestrial global productivity: past, present and future*. Academic, London, pp 401–428
- Hall SJ, Matson PA (1999) Nitrogen oxide emissions after nitrogen additions in tropical forests. *Nature* 400:1997–2000
- Haran S, Ogendra S, Seska M, Bratanova M, Raskin I (2000) Characterization of Arabidopsis acid phosphatase promoter and regulation of acid phosphatase expression. *Plant Physiol* 124:615–626
- Harrington RA, Fownes JH, Vitousek PM (2001) Production and resource use efficiencies in N- and P-limited tropical forests: a comparison of responses to long-term fertilization. *Ecosystems* 4:646–657
- Harrison A (1987) *Soil organic phosphorus: a review of world literature*. CABI, Wallingford, UK
- Hassink J (1997) The capacity of soils to preserve organic C and N by their association with clay and silt particles. *Plant Soil* 191:77–87
- Hayes J, Richardson A, Simpson R (2000) Components of organic phosphorus in soil extracts that are hydrolysed by phytase and acid phosphatase. *Biol Fertil Soils* 32:279–286
- Hedin L, Armesto J, Johnson A (1995) Patterns of nutrient loss from unpolluted, old growth temperate forests-evaluation of biogeochemical theory. *Ecology* 76:493–509

- Hedin LO, Vitousek PM, Matson PA (2003) Nutrient losses over four million years of tropical forest development. *Ecology* 84:2231–2255
- Herbert DA, Fownes JH (1995) Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry* 29:223–235
- Herrera R, Merida T, Stark N, Jordan C (1978) Direct phosphorus transfer from leaf litter to roots. *Naturwissenschaften* 65:208–209
- Hobbie S, Vitousek PM (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology* 81:1867–1877
- Hooper DU, Johnson L (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46:247–293
- Horst W, Kamh M, Jibrin J, Chude V (2001) Agronomic measures for increasing P availability to crops. *Plant Soil* 237:211–223
- Houlton BZ, Wang YP, Vitousek PM, Field CB (2008) A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454:327–330
- Husband R, Herre E, Turner S, Gallery R, Young J (2002) Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. *Mol Ecol* 11:2669–2678
- Janos DP (1980) Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. *Ecology* 61:151–162
- Jansa J, Finlay R, Wallander H, Smith FA, Smith SE (2011) Role of mycorrhizal symbioses in phosphorus cycling. In: Bünenmann E, Oberson A, Frossard E (eds) *Phosphorus in action: biological processes in soil phosphorus cycling*. Soil biology, vol 26. Springer, Heidelberg. doi: 10.1007/978-3-642-15271-9_6
- Jenny H (1941) *Factors of soil formation*. McGraw-Hill, New York, NY
- Jobbagy E, Jackson R (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10:423–436
- Johnson RA, Frizano J, Vann DR (2003) Biogeochemical implications of labile phosphorus in forest soils determined by the Hedley fractionation procedure. *Oecologia* 135:487–499
- Keller M, Kaplan W, Wofsy S (1986) Emissions of N₂O, CH₄, and CO₂ from tropical soils. *J Geophys Res* 91:11791–11801
- Kitayama K, Aiba S (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *J Ecol* 90:37–51
- Kitayama K, Majalap-Lee N, Aiba S (2000) Soil phosphorus fractionation and phosphorus-use efficiencies of tropical rainforests along altitudinal gradients of Mount Kinabalu, Borneo. *Oecologia* 123:342–349
- Kitayama K, Aiba S, Takyu M, Majalap N, Wagai R (2004) Soil phosphorus fractionation and phosphorus-use efficiency of a Bornean tropical montane rain forest during soil aging with podzolization. *Ecosystems* 7:259–274
- Kroehler C, Linkins A (1988) The root surface phosphatases of *Eriophorum vaginatum* – effects of temperature, pH, substrate concentration and inorganic phosphorus. *Plant Soil* 105:3–10
- Kroehler C, Linkins A (1991) The absorption of inorganic-phosphate from 32P-labeled inositol hexaphosphate by *Eriophorum vaginatum*. *Oecologia* 85:424–428
- Lajtha K, Harrison A (1995) Strategies of phosphorus acquisition and conservation by plant species and communities. In: Tiessen H (ed) *Phosphorus in the global environment*. Wiley, Chichester, UK
- Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. *Trends Ecol Evol* 23:95–103
- LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89:371–379
- Lewis WM Jr, Saunders JF III, Levine SN, Weibezahn FH (1986) Organic carbon in the Caura River, Venezuela. *Limnol Oceanogr* 31:653–656

- Lewis SL, Lopez-Gonzalez G, Sonke B, Affum-Baffoe K, Baker TR, Ojo LO, Phillips OL, Reitsma JM, White L, Comiskey JA, Djuikouo M-N, Ewango CEN, Feldpausch TR, Hamilton AC, Gloor M, Hart T, Hladik A, Lloyd J, Lovett JC, Makana J-R, Malhi Y, Mbago FM, Ndangalasi HJ, Peacock J, Peh KS-H, Sheil D, Sunderland T, Swaine MD, Taplin J, Taylor D, Thomas SC, Votere R, Wöll H (2009) Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–1006
- Likens G, Bormann F (1995) *Biogeochemistry of a forested ecosystem*. Springer, New York, NY
- Linquist B, Singleton P, Yost R, Cassman K (1997) Aggregate size effects on the sorption and release of phosphorus in an ultisol. *Soil Sci Soc Am J* 61:160–166
- Liptzin D, Silver WL (2009) Effects of carbon additions on iron reduction and phosphorus availability in a humid tropical forest soil. *Soil Biol Biochem* 41:1696–1702
- Lopez-Bucio J, Hernandez-Abreu E, Sanchez-Calderon L, Perez-Torres A, Rampey R, Bartel B, Herrera-Estrella L (2005) An auxin transport independent pathway is involved in phosphate stress-induced root architectural alterations in *Arabidopsis*. Identification of BIG as a mediator of auxin in pericycle cell activation. *Environ Stress Adapt* 137:681–691
- Ma Z, Bielenberg G, Brown K, Lynch J (2001) Regulation of root hair density by phosphorus availability in *Arabidopsis thaliana*. *Plant Cell Environ* 24:459–467
- Maheswaran J, Gunatilleke I (1990) Nitrogenase activity in soil and litter of a tropical lowland rain forest and an adjacent fernland in Sri Lanka. *J Trop Ecol* 6:281–289
- Mahowald NM, Artaxo P, Baker AR, Jickells TD, Okin GS, Randerson JT, Townsend AR (2005) Impacts of biomass burning emissions and land use change on Amazonian atmospheric phosphorus cycling and deposition. *Global Biogeochem Cycles* 19:GB4030
- Malhi Y, Aragao LEOC, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P (2009) Exploring the likelihood of a climate-change-induced dieback of the Amazon rainforest. *Proc Natl Acad Sci USA* 106:20610–20615
- Markewitz D, Davidson E, Moutinho P, Nepstad D (2004) Nutrient loss and redistribution after forest clearing on a highly weathered soil in Amazonia. *Ecol Appl* 14:S177–S199
- Markewitz D, Resende JCF, Parron L, Bustamante M, Klink CA, RdO F, Davidson EA (2006) Dissolved rainfall inputs and streamwater outputs in an undisturbed watershed on highly weathered soils in the Brazilian cerrado. *Hydrol Process* 20:2615–2639
- Martinelli L, Piccolo M, Townsend A, Vitousek P, Cuevas E, McDowell W, Robertson G, Santos O, Treseder K (1999) Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests. *Biogeochemistry* 46:45–65
- Matson PA, Vitousek PM (1990) Ecosystem approach to a global nitrous oxide budget. *Bioscience* 40:667–672
- Matson P, Vitousek P, Ewel J, Mazzarino M, Robertson G (1987) Nitrogen transformation following tropical forest felling and burning on a volcanic soil. *Ecology* 68:491–502
- McDowell WH, Lugo AE, James A (1995) Export of nutrients and major ions from Caribbean catchments. *J N Am Benthol Soc* 14:12–20
- McGill WB, Cole CV (1981) Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. *Geoderma* 26:267–286
- McGrath DA, Smith CK, Gholz HL, Oliveira FD (2001) Effects of land-use change on soil nutrient dynamics in Amazonia. *Ecosystems* 4:625–645
- McGroddy M, Daufresne T, Hedin L (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology* 85:2390–2401
- McKane R, Johnson L, Shaver G, Nadelhoffer K, Rastetter E, Fry B, Giblin A, Kielland K, Kwiatkowski B, Laundre J, Murray G, Turner B, Condon L, Richardson S, Peltzer D, Allison V (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415:68–71
- McLachlan K (1980) Acid phosphatase activity of intact roots and phosphorus nutrition in plants. I. Assay conditions and phosphatase activity. *Aust J Agric Res* 3:429–440
- Merckx R, Den Hartog A, van Veen J (1985) Turnover of root-derived material and related microbial biomass formation in soils of different texture. *Soil Biol Biochem* 17:565–569

- Miller S, Liu J, Allan D, Menzhuber C, Fedorova M, Vance C (2001) Molecular control of acid phosphatase secretion into the rhizosphere of proteoid roots from phosphorus-stressed white lupin. *Plant Physiol* 127:594–606
- Moorhead D, Kroehler C, Linkins A, Reynolds J (1993) Extracellular acid phosphatase activities in *Eriophorum vaginatum* tussocks – a modeling synthesis. *Arctic Alpine Res* 25:50–55
- Moulin C, Chiapello I (2006) Impact of human-induced desertification on the intensification of Sahel dust emission and export over the last decades. *Geophys Res Lett* 33:L18808
- Nannipieri P, Giagnoni L, Landi L, Renella G (2011) Role of phosphatase enzymes in soil. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. *Soil biology*, vol 26. Springer, Heidelberg. doi: [10.1007/978-3-642-15271-9_9](https://doi.org/10.1007/978-3-642-15271-9_9)
- Neff JC, Reynolds R, Fernandez D, Lamothe P (2006) Controls of bedrock geochemistry on soil and plant nutrients in southeastern Utah. *Ecosystems* 9:879–893
- Neill C, Piccolo MC, Stuedler PA, Cerff CC (1995) Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon basin. *Soil Biol Biochem* 27:1167–1175
- Neill C, Deegan LA, Thomas SM, Cerri CC (2001) Deforestation for pasture alters nitrogen and phosphorus in small Amazonian streams. *Ecol Appl* 11:1817–1828
- Newberry D, Alexander L, Rother J (1997) Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. *Ecol Monogr* 67:367–409
- Oades J, Waters A (1991) Aggregate hierarchy in soils. *Aust J Agric Res* 29:815–828
- Oberson A, Friesen DK, Morel C, Tiessen H (1997) Determination of phosphorus released by chloroform fumigation from microbial biomass in high P sorbing tropical soils. *Soil Biol Biochem* 29:1579–1583
- Oberson A, Friesen DK, Rao IM, Bühler S, Frossard E (2001) Phosphorus transformations in an Oxisol under contrasting land-use systems: the role of soil microbial biomass. *Plant Soil* 237:197–210
- Oehl F, Oberson A, Sinaj S, Frossard E (2001) Organic phosphorus mineralization studies using isotopic dilution techniques. *Soil Sci Soc Am J* 65:780–787
- Okin GS, Mahowald N, Chadwick OA, Artaxo P (2004) Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. *Glob Biogeochem Cycles* 18:GB2005
- Olander L, Vitousek P (2000) Regulation of soil phosphatase and chitinase activity by N and P availability. *Biogeochemistry* 49:175–190
- Olander L, Vitousek PM (2004) Biological and geochemical sinks for phosphorus in soil from a wet tropical forest. *Ecosystems* 7:404–419
- Palm C, Sanchez P, Ahamed S, Awiti A (2007) Soils: a contemporary perspective. *Annu Rev Environ Resour* 32:99–129
- Pant H, Edwards A, Vaughan D (1994) Extraction, molecular fractionation and enzyme degradation of organically associated phosphorus in soil solutions. *Biol Fertil Soils* 17:196–200
- Paoli GD, Curran LM, Slik JWF (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia* 155:287–299
- Parton W, Neff J, Vitousek P (2005) Modeling phosphorus, carbon, and nitrogen dynamics in terrestrial ecosystems. In: Turner B, Frossard E, Baldwin D (eds) *Organic phosphorus in the environment*. CABI, Wallingford, UK
- Paul E, Clark F (1989) *Soil microbiology and biochemistry*. Academic, San Diego, CA
- Pearson HL, Vitousek PM (2002) Soil phosphorus fractions and symbiotic nitrogen fixation across a substrate-age gradient in Hawaii. *Ecosystems* 5:587–596
- Phillips OL, Malhi Y, Higuchi N, Laurance WF, Nu PV, Va RM, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442
- Phillips OL, Lewis SL, Baker TR, Chao K-J, Higuchi N (2008) The changing Amazon forest. *Philos Trans R Soc B* 363:1819–1827
- Raghothama K (1999) Phosphate acquisition. *Annu Rev Plant Physiol Plant Mol Biol* 50:665–693

- Raich J, Schlesinger W (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B:81–99
- Reed SC, Cleveland CC, Townsend AR (2007) Controls over leaf litter and soil nitrogen fixation in two lowland tropical rain forests. *Biotropica* 39:585–592
- Reed SC, Cleveland CC, Townsend AR (2008) Tree species control rates of free-living nitrogen fixation in a tropical rain forest. *Ecology* 89:2924–2934
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc Natl Acad Sci USA* 101:11001–11006
- Richter DD, Allen L, Li J, Markewitz D, Raikes J (2006) Bioavailability of slowly cycling soil phosphorus: major restructuring of soil P fractions over four decades in an aggrading forest. *Oecologia* 150:259–271
- Sanchez P (1976) Properties and management of soils in the tropics. Wiley, New York, NY
- Sanchez PA, Bandy DE, Villachica JH, Nicholaides JJ (1982) Amazon basin soils: management for continuous crop production. *Science* 216:821–827
- Saunders T, McClain M, Llerena C (2006) The biogeochemistry of dissolved nitrogen, phosphorus, and organic carbon along terrestrial-aquatic flowpaths of a montane headwater catchment in the Peruvian Amazon. *Hydrol Process* 20:2549–2562
- Schachtman D, Reid R, Ayling S (1998) Phosphorus uptake by plants: from soil to cell. *Plant Physiol* 116:447–453
- Schlesinger W (1997) Biogeochemistry: an analysis of global change. Academic, San Diego, CA
- Schuur EAG, Matson PA (2001) Net primary productivity an nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia* 128:431–442
- Silver W, Scatena F, Johnson A, Siccama T, Sanchez M (1994) Nutrient availability in a montane wet tropical forest: Spatial patterns and methodological considerations. *Plant Soil* 164:129–145
- Silver WL, Lugo AE, Keller M (1999) Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* 44:301–328
- Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. *Plant Soil* 241:155–176
- Skene KR (1998) Cluster roots: some ecological considerations. *J Ecol* 86:1060–1064
- Soil Survey Staff (2006) Keys to soil taxonomy. Natural Resources Conservation Service, US Department of Agriculture, Washington, DC
- Sollins P, Robertson GP, Uehara G (1988) Nutrient mobility in variable- and permanent-charge soils. *Biogeochemistry* 6:181–199
- Stallard RF, Edmond JM (1983) Geochemistry of the Amazon. 2. The influence of geology and weathering environment on the dissolved load. *J Geophys Res* 88(C14):9671–9688
- Stark NM, Jordan CF (1978) Nutrient retention by the root mat of an Amazonian rain forest. *Ecology* 59:434–437
- Stephens BB, Gurney KR, Tans PP, Sweeney C, Peters W, Bruhwiler L, Ciais P, Ramonet M, Bousquet P, Nakazawa T, Aoki S, Michida T, Inoue G, Vinnichenko N, Lloyd J, Jordan A, Heimann M, Shibistova O, Langenfelds R, Steele LP, Francey RJ, Denning AS (2007) Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂. *Science* 316:1732–1735
- Swap R, Garstang M, Greco S, Talbot R, Kallberg P (1992) Saharan dust in the Amazon basin. *Tellus B Chem Phys Meteorol* 44:133–149
- Swift M, Heal O, Anderson J (1979) Decomposition in terrestrial ecosystems. *Studies in ecology*, vol 5. University of California Press, Berkeley, CA
- Tanner E, Kapos V, Franco W (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73:78–86
- Tarafdar J, Jungk A (1987) Phosphatase activity in the rhizosphere and its relation to the depletion of soil organic phosphorus. *Biol Fertil Soils* 3:199–204
- Tarnocai C, Canadell J, Schuur E, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Glob Biogeochem Cycles* 23:GB2023

- ter Steege H, Pitman NC, Phillips OL, Chave J, Sabatier D, Duque A, Spichiger R, Va R (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443:444–447
- Theodorou ME, Plaxton WC (1996) Metabolic adaptations of plant respiration to nutritional phosphate deprivation. *Plant Physiol* 101:339–344
- Thornton P, Doney S, Lindsay K, Moore J, Mahowald N, Randerson J, Fung I, Lamarque J, Feddesma J, Lee Y (2009) Carbon-nitrogen interactions regulate climate-carbon feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences* 6:2099–2120
- Tiessen H, Moir JO (1993) Characterization of available P by sequential extraction. In: Carter M (ed) *Soil sampling and methods of analysis*. Lewis, Ann Arbor, MI
- Tiessen H, Stewart J, Cole C (1984) Pathways of phosphorus transformations in soils of differing pedogenesis. *Soil Sci Soc Am J* 48:853–858
- Townsend AR, Cleveland CC, Asner GP, Bustamante MM (2007) Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88:107–118
- Townsend AR, Asner GP, Cleveland CC (2008) The biogeochemical heterogeneity of tropical forests. *Trends Ecol Evol* 23:424–431
- Toy ADF (1973) *The chemistry of phosphorus*. Pergamon, Oxford
- Treseder K, Vitousek P (2001) Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology* 82:946–954
- Turner BL (2008) Resource partitioning for soil phosphorus: a hypothesis. *J Ecol* 96:698–702
- Uehara G, Gillman G (1980) Charge characteristics of soils with variable and permanent charge minerals. 1. Theory. *Soil Sci Soc Am J* 44:250–252
- Uhde-Stone C, Gilbert G, Johnson J, Litjens R, Zinn K, Temple S, Vance C, Allan D (2004) Acclimation of white lupin to phosphorus deficiency involves enhanced expression of genes related to organic acid metabolism. *Plant Soil* 248:99–116
- Vance C, Uhde-Stone C, Allan D (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol* 157:423–447
- Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. *Am Nat* 119:553–572
- Vitousek PM (1984) Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* 65:285–298
- Vitousek PM (2004) *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton University Press, Princeton, NJ
- Vitousek PM, Farrington H (1997) Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry* 37:63–75
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87–115
- Vitousek PM, Reiners W (1975) Ecosystem succession and nutrient retention hypothesis. *Bioscience* 25:376–381
- Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forest. *Annu Rev Ecol Syst* 17:137–167
- Vitousek P, Chadwick O, Matson P, Allison S, Derry L, Kettley L, Luers A, Mecking E, Monastera V, Porder S (2003) Erosion and the rejuvenation of weathering-derived nutrient supply in an old tropical landscape. *Ecosystems* 6:762–772
- Wada K (1985) The distinctive properties of andisols. *Adv Soil Sci* 2:174–229
- Walker T, Syers J (1976) The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19
- Wardle D, Walker L, Bardgett R (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305:509–513
- Wasaki J, Maruyama H (2011) Molecular approaches to the study of biological phosphorus cycling. In: Bünemann E, Oberson A, Frossard E (eds) *Phosphorus in action: biological processes in soil phosphorus cycling*. *Soil biology*, vol 26. Springer, Heidelberg. doi: [10.1007/978-3-642-15271-9_4](https://doi.org/10.1007/978-3-642-15271-9_4)

- Wasaki J, Omura M, Ando M, Dateki H, Shinano T, Osaka M, Ito H, Matsui H, Tadano T (2000) Molecular cloning and root specific expression of secretory acid phosphatases from phosphate-deficient lupin (*Lupinus albus* L.). *Soil Sci Plant Nutr* 46:427–437
- White G, Zelazny L (1986) Charge properties of soil colloids. In: Sparks D (ed) *Soil physical chemistry*. CRC, Boca Raton, FL, pp 39–81
- Whitton B, Al-Shehri A, Ellwood N, Turner B (2005) Ecological aspects of phosphatase activity in cyanobacteria, eukaryotic algae and bryophytes. In: Turner BL, Frossard E, Baldwin D (eds) *Organic phosphorus in the environment*. CABI, Wallingford, UK, pp 205–241
- Wieder W, Cleveland CC, Townsend AR (2009) Controls over leaf litter decomposition in wet tropical forests. *Ecology* 90:3333–3341
- Wilcke W, Yasin S, Valarezo C, Zech W (2001) Change in water quality during the passage through a tropical montane rain forest in Ecuador. *Biogeochemistry* 55:45–72
- Williams MR, Melack JM (1997) Solute export from forested and partially deforested catchments in the central Amazon. *Biogeochemistry* 38:67–102
- Xuluc-Talosa F, Vester H, Ramirez-Marcial N, Castellanos-Albores J, Lawrence D (2003) Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. *For Ecol Manag* 174:401–412
- Yuan ZY, Chen HY (2009) Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Glob Ecol Biogeogr* 18:11–18
- Zou X, Binkley D, Doxtader K (1992) A new method for estimating gross phosphorus mineralization and immobilization rates in soils. *Plant Soil* 147:243–250
- Zou X, Binkley D, Caldwell B (1995) Effects of dinitrogen-fixing trees on phosphorus biogeochemical cycling in contrasting forests. *Soil Sci Soc Am J* 59:1452–1458