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Soil acidification and adaptations of plants and microorganisms in Bornean tropical forests

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Abstract In tropical forest ecosystems, a paradoxical relationship is commonly observed between massive biomass production and low soil fertility (low pH). The loss and deficiency of soil phosphorus (P) and bases generally constrain biomass production; however, high productivity on nutrient-deficient soils of Bornean tropical forests is hypothesized to be maintained by plant and microorganism adaptation to an acidic soil environment. Proton budgets in the plant–soil system indicated that plants and microorganisms promote acidification to acquire bases, even in highly acidic tropical soils. The nitric and organic acids they produce contribute to the mobilization of basic cations and their uptake by plants. In response to soil P deficiency and the recalcitrance of lignin-rich organic matter, specific trees and fungi can release organic acids and enzymes for nutrient acquisition. Organic acids exuded by roots and rhizosphere microorganisms can promote the solubilization of P bonded to aluminum and iron oxides and its uptake by plants from P-poor soils. Lignin degradation, a rate-limiting step in organic matter decomposition, is specifically enhanced in acidic organic layers by lignin peroxidase, produced by white-rot fungi, which may solubilize recalcitrant lignin and release soluble aromatic substances into the soil solution. This dissolved organic matter functions in the transport of nitrogen, P, and basic cations in acidic soils without increasing leaching loss. In Bornean tropical forests, soil acidification is promoted by plants and microorganisms as a nutrient acquisition strategy, while plant roots and fungi can develop rhizosphere and enzymatic processes that promote tolerance of low pH.

Keywords Dissolved organic carbon · Lignolysis · Organic acids · Rhizosphere · Soil organic matter

Introduction

Why can tropical forests maintain high productivity in highly weathered soils? Paradoxical relationships between high biomass productivity and low soil fertility have been reported for several tropical forest ecosystems (Whittaker 1975; Terborgh 1992). Because large amounts of precipitation increase soil acidification and nutrient loss through weathering and leaching (Jenny 1941; Fujii et al. 2010a), water and nutrient availability to plants are often incompatible in terrestrial ecosystems (Zhou et al. 2009). High precipitation generally favors for high biomass production, but soil acidification induces deficiencies of nutrients, phosphorus (P), and bases as well as aluminum (Al) toxicity. Low pH and nutrient deficiency generally limit plant production on acidic soils, especially that of crop species (Kochian et al. 2004). However, the aboveground biomass of some tropical tree species in Southeast Asia has been reported to increase along with soil acidification (van Schaik and Mirmanto 1985). The mechanisms of nutrient acquisition in tropical forests on acidic soil environments need to be clarified.

Because the levels of bases and P decrease through weathering and stabilization within organic matter and clays (Walker and Syers 1976; Anderson 1988), their available pools in tropical soils are typically smaller than those in temperate forest soils with similar geology (Sollins 1998). However, controversy exists as to whether “soil fertility” is critical for tropical forests (Jordan and Herrera 1981; Vitousek and Sanford 1986). Several studies on soil weathering sequences have shown that nutrient deficiency can eventually limit net primary production (NPP) in most tropical forests (Schoor and Matson 2001; Austin 2002; Wardle et al. 2004). In Southeast Asia, however, tropical forests can support substantial aboveground biomass and NPP, which are

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comparable to or greater than those in the other tropical forests of America and Africa, even on acidic and nutrient (P or bases)-limited soils (Brown 1997; Kitayama et al. 2000; Slik et al. 2013). The high productivity of these tropical forests can generally be explained by the development of efficient nutrient cycling mechanisms: rapid turnover of nutrients, resorption, mycorrhizal associations, and diversity of tropical soils and tree species (Vitousek and Sanford 1986; Kitayama 2005). Tree species diversity and niche partitioning (edaphic specialization) can also ameliorate the effects of nutrient deficiency on forest productivity (Paoli et al. 2006; Cavanaugh et al. 2014). For example, shifts in plant community structure toward efficient P utilizers may allow for the maintenance of high biomass production even in P-limited environments (Kitayama 2005).

Regarding specific aspects in Southeast Asia, Ashton (1988) hypothesized that Dipterocarpaceae exhibit high species diversity, tall stature, and large biomass production through adaptation to acidic soils via ectomycorrhizal associations. The high host specificity of ectomycorrhizae can cause competitive advantage and family-level monodominance of Dipterocarpaceae in Southeast Asia, whereas most of the dominant trees in America and Africa associate with vesicular-arbuscular mycorrhizae (Connell and Lowman 1989). High productivity on nutrient-deficient soils in Bornean tropical forests is hypothesized to be maintained by the adaptation of plants and microorganisms to the acidic soil environment. However, low pH generally limits their abilities to acquire nutrients via solubilization, decomposition, and uptake (Kochian et al. 2004; Hayakawa et al. 2013). Further, low pH increases recalcitrance of soil organic P to microbial mineralization and decreases P solubility (Turner and Engelbrecht 2011). Therefore, understanding how plant roots and microorganisms can survive and acquire nutrients in the acidic soils of Bornean tropical forests is essential.

Some plants can cope with nutrient deficiency in acidic soils via modifications to their root morphologies and in their nutrient uptakes and metabolisms (Hammond et al. 2004). However, because large proportions of nutrients are stabilized in non-labile form by bonding to clays (oxides) or recalcitrant organic matter (lignin-like aromatic compounds), their solubilization is a prerequisite for uptake by plant roots and microorganisms. To solubilize recalcitrant nutrients, plant roots and microorganisms can release organic acids and enzymes into the soil solution (Landeweert et al. 2001; Sinsabaugh et al. 2002; van Schöll et al. 2008). In Bornean tropical forests, three questions remain to be answered: (1) whether plants can acquire enough basic cations to meet the demands of high NPP, (2) whether roots and ectomycorrhizal fungi can release large amounts of organic acids into the rhizosphere in response to P deficiency, and (3) whether fungi can produce specific enzymes (e.g., lignin peroxidase) to enhance decomposition of the recalcitrant organic matter (lignin) of dipterocarp species under acidic conditions.

Because most nutrient solubilization reactions occur in the soil solution and on solid soil (Ugolini and Sletten 1991), the strategies by which plants and microorganisms acquire nutrients from acidic soils can be elucidated by tracing the dynamics of acids (e.g., carbonic and organic acids) and enzymes released into the soil solution. This paper reviews the progress of knowledge on these adaptive mechanisms to test the hypothesis that high productivity on nutrient-deficient soils of Bornean tropical forests can be maintained by the adaptation of plants and microorganisms to an acidic soil environment.

Soil acidification as revealed by proton budgets in a Bornean tropical forest

Diverse tropical forests share the requirement that most of the plants and microorganisms must survive in acidic soils. Acidic soils (pH < 5.5) are widespread, especially in humid regions; they cover 30 % of the world's total land area and 60 % of the total area in the tropics (Sanchez and Logan 1992). Soil acidification is a natural result of long-term weathering in climates where precipitation exceeds evapotranspiration (Krug and Frink 1983; Hallbäcken and Tamm 1986), but it is also an ongoing biological process driven by nitrification, the dissociation of organic acids and carbonic acid, and the excess uptake of cations over anions by plants (van Breemen et al. 1983; Binkley and Richter 1987). The extent of soil acidification can vary from ecosystem to ecosystem, depending on the kinds and amounts of proton sources (van Breemen et al. 1984; Guo et al. 2010). In several tropical forests from America, the production and leaching of carbonic acids from intensive root and microbial respiration has been reported to be a major cause of soil acidification (Johnson 1977; McDowell 1998). The hypothesis has been proposed that carbonic acid leaching has developed in tropical forests to utilize high soil CO₂ pressure to acquire exchangeable bases and to minimize leaching losses of bases from base-poor soils (Johnson 1977). However, in Southeast Asian tropical forests, nutrient acquisition of trees in the Ultisol soils may be different from those in the Oxisol and Ultisol soils of America and Africa, in that Asian Ultisol soils are richer in weatherable minerals because of steep slopes or relatively young geological ages (Fujii et al. 2011a).

To investigate the site-specific and common aspects of acidification between tropical forests, the dominant soil-acidifying processes were analyzed using proton budgets in an acidic Ultisol soil in East Kalimantan, Indonesia (Fujii et al. 2008, 2010a). The roles of plants and microorganisms in proton generation and consumption can be quantified using the input-output budgets of ions in each soil layer (Table 1; van Breemen et al. 1983, 1984). Litter and wood biomasses contain more cations than anions, resulting in proton release from roots (Fig. 1; Table 1). Based on ion fluxes in

Table 1 Proton-generating and -consuming processes in soils

H ⁺ budget	Major processes	Representative reaction	Proton budget calculation
(1) H ⁺ input (e.g. acid rain)			H ⁺ input = (H ⁺) _{in} - (H ⁺) _{out}
(2) Cation excess uptake by plants	Cation uptake	Ca ²⁺ + 2R-OH → (R-O) ₂ Ca (plant) + 2H ⁺	NPG _{Bio} = (Cat) _{bio} - (Ani) _{bio}
	Anion uptake	H ₂ PO ₄ ⁻ + H ⁺ + R-OH → R-H ₂ PO ₄ (plant) + H ₂ O	
(3) N transformation	Mineralization	R-NH ₂ (organic matter) + H ₂ O + H ⁺ → R-OH + NH ₄ ⁺	NPG _{Ntr} = (NH ₄ ⁺) _{in} - (NH ₄ ⁺) _{out} + (NO ₃ ⁻) _{out} - (NO ₃ ⁻) _{in}
	Nitrification	NH ₄ ⁺ + H ₂ O → NO ₃ ⁻ + 2H ⁺ + H ₂ O	
	Ammonium uptake	R-OH + NH ₄ ⁺ → R-NH ₂ (plant) + H ₂ O + H ⁺	
	Nitrate uptake	R-OH + NO ₃ ⁻ + H ⁺ → R-NH ₂ (plant) + 2O ₂	
(4) Dissociation of carbonic acid	Dissociation	H ₂ CO ₃ → HCO ₃ ⁻ + H ⁺	NPG _{Car} = (HCO ₃ ⁻) _{out} - (HCO ₃ ⁻) _{in}
	Protonation	HCO ₃ ⁻ + H ⁺ → H ₂ CO ₃	
(5) Dissociation of organic acid	Dissociation	2CH ₂ O + 3/2O ₂ → HC ₂ O ₄ ⁻ + H ⁺ + H ₂ O	NPG _{Org} = (Org ⁿ⁻) _{out} - (Org ⁿ⁻) _{in}
	Protonation, mineralization, sorption	HC ₂ O ₄ ⁻ + H ⁺ + 1/2 O ₂ → 2 CO ₂ + H ₂ O	
(6) Weathering and cation exchange reaction	Dissolution of bases	RCOO ⁻ + H ⁺ + Al-OH → Al-COOR + H ₂ O K ₂ O _(s) + 2H ⁺ → 2 K ⁺ + H ₂ O	ΔANC = {(Cat) _{in} - (Cat) _{out} - (Cat) _{bio} } - {(Ani) _{in} - (Ani) _{out} - (Ani) _{bio} }
	Weathering of feldspar to kaolinite	2 KAlSi ₃ O ₈ + 2H ⁺ + 9H ₂ O → Al ₂ Si ₂ O ₅ (OH) ₄ + 2K ⁺ + 4H ₄ SiO ₄	

The suffixes “in” and “out” represent ion fluxes entering the soil horizon (e.g., throughfall for the O horizon) and leaving the horizon, respectively.

The suffix “bio” represents ion fluxes caused by vegetation uptake (wood increment and litterfall)

Cat and Ani represent cations (Na⁺, K⁺, Mg²⁺, Ca²⁺, Fe³⁺, Alⁿ⁺) and anions (Cl⁻, SO₄²⁻, H₂PO₄⁻), respectively

The suffixes “Ntr”, “Car”, and “Org” represent N transformation, Carbonic acid, and Organic acid, respectively

ΔANC represents a decrease in the acid neutralizing capacity (ANC) of the soil solid phase, soil acidification rate

Acid neutralizing capacity (ANC) was defined as sum of basic cation equivalence minus sum of strongly acidic anion equivalence of the solid phase of soil

ANC = 2(Na₂O) + 2(K₂O) + 2(MgO) + 2(CaO) + 2(FeO) + 6(Al₂O₃) - 2(SO₃) - 2(P₂O₅) - (HCl), where parentheses denote total molar concentration

precipitation and soil solutions, the production of organic acids and nitrate (NO₃⁻) in the canopy and organic layers also contributed to proton generation, the mobilization of basic cations, and soil acidification (Fig. 1). In the mineral soil horizons, protons were neutralized by the mineralization of organic acids, nitrate uptake by plants, and the release of basic cations by weathering (Fig. 1; Table 1). The contribution of carbonic acid to soil acidification was minor in the Bornean tropical soil studied (Fujii et al. 2009), and the dominance of organic versus carbonic acid leaching appeared to depend on soil solution pH and the production of dissolved organic matter (sources of organic acids), which will be discussed later.

The organic, carbonic, and nitric acids produced by root and microbial activities commonly contribute to the mobilization of basic cations in the soil and their accumulation in plant biomass. Acidification was apparently promoted by plants and microorganisms, even in the highly acidic soils of Bornean tropical forests (Fujii et al. 2009a). This conclusion is supported by two findings: first, most mineral weathering reactions require acidification to release basic cations (Table 1), and second, most plants require more cations than and release pro-

tons to maintain the charge balance in their tissues. The production nitric and organic acids may not be intentional by plant communities but rather the consequences of multiple processes. However, the energy for proton generation is derived ultimately from the high organic matter production in tropical forests. Furthermore, the magnitude of proton generation in forest soils is regulated by the production and decomposition of organic matter, as well as the leaching intensity of water, unlike in cropland soils, where acidification is caused by the leaching losses of nitrate and bases (Guo et al. 2010; Fujii et al. 2009a, 2012a). Therefore, soil acidification can be regarded at an ecosystem scale as an adaptive process of trees for nutrient acquisition, at least in Bornean tropical soils containing weatherable minerals.

Al toxicity and P deficiency caused by soil acidification in tropical forests

Soil acidification enhances Al toxicity and P limitation though geochemical and biological processes (Kochian et al. 2004). The Al solubility and toxicity increases at low soil pH (pH < 4.5), whereas P solubility decreases.

Fig. 1 Generation and consumption of protons in soil of the Bukit Soeharto Experimental Forest in East Kalimantan, Indonesia. The white arrows indicate proton generation, whereas the shaded arrows indicate proton consumption. Data from Fujii et al. (2009a, 2010a)

The high Al concentration is toxic to roots and soil microorganisms (Jentschke et al. 2001; Illmer and Mutschlechner 2004) and deactivates enzymes (Scheel et al. 2008). Limited P can inhibit NPP in tropical forests via several factors: low availability of P relative to nitrogen (N), soil weathering, and P-deficient bedrock (Vitousek and Howarth 1991; Vitousek et al. 2010). The rapid mineralization of soil organic matter in tropical forests can increase N availability to plants relative to that in N-limited temperate forests, where the slow decomposition of recalcitrant organic matter (e.g., lignin) leads to the accumulation of humified materials (Takeda 1995). However, the pool size of soil P, which is largely derived from bedrock, can typically decrease with intense weathering and leaching in tropical forests (Walker and Syers 1976).

In Bornean tropical forests, decreases in pool sizes of total P were reported for highly-weathered Ultisol and Spodosol soils (Kitayama et al. 2000, 2004). Furthermore, the proportion of non-labile P to total soil P is increased by its incorporation into organic matter and sorption onto Al and iron (Fe) oxides and clays in acidic tropical soils. Regarding stabilization of the soil organic P fraction, occlusion of P within recalcitrant humic substances is greater at low pH (Turner et al. 2007; Turner and Engelbrecht 2011). Although inorganic P can be supplied by microbial mineralization of labile organic P (e.g., DNA) and the release of ester-bonded P, solution P is rapidly removed by sorption onto Al and Fe oxides and chemical precipitation in acidic soils (Turner and Engelbrecht 2011). Therefore, recycling of the organic P pool may be insufficient to maintain high NPP in tropical forests (McGroddy et al. 2008). Because

soil P is the only ultimate source of P to plants, mining (dissolution) of the occluded P within oxides or clays is necessary for plants to maintain a P supply in acidic soils (Treseder and Vitousek 2001; Liu et al. 2006).

Tropical plants have developed two types of adaptive strategies for P deficiency: (1) those that enhance P conservation and use efficiency, and (2) those that enhance P acquisition and uptake (Kitayama 2013). Some plant species stringently recycle P through ectomycorrhizal and fine root systems (Jordan and Herrera 1981; Lambers et al. 2008) and increase P resorption before leaf abscission (Kitayama et al. 2004; Hidaka and Kitayama 2011). With respect to P acquisition, plant roots and microorganisms can use non-labile P through the exudation of organic acids and enzymes. Organic acids are indispensable for complexation with Al(Fe) in acidic soils, so their release from roots is considered to be the most common and efficient strategy for both Al detoxification and P acquisition in the humid tropics (Ma et al. 2001). In humid Asia, some cultivars of barley have within the last 3,000 years evolved a genetic mechanism for releasing organic acids as an adaptation to Al toxicity in acidic soils (Fujii et al. 2012). Some plant species (e.g., *Banksia* and *Lupinus*) can develop fine root systems such as cluster roots (or proteoid roots) with increased organic acid exudation (Jones 1998; Neumann et al. 2000). In Bornean tropical forests, the exudation of organic acids from roots and fungi can promote the solubilization of P occluded in Al and Fe oxides and its uptake by plants from P-limited soils, as discussed in the following two sections. Roots, as well as soil microorganisms, can release enzymes (e.g., acid phosphatase) that mineralize soil organic P. Several studies have reported that root phosphatase activity can also increase in response to P deficiency (Nannipieri et al. 2011; Kitayama 2013).

Organic exudation from roots in rhizospheres of P-poor soils in Bornean tropical forests

Low-molecular-weight organic acids, especially oxalic, citric, and malic acids, can solubilize recalcitrant P bound to Al and Fe oxides (Johnson and Loeppert 2006). Plant roots release organic acids through slow passive diffusion (Jones 1998; Jones et al. 2004), but some species can greatly increase root exudation in response to P deficiency (Ström et al. 1994; Grayston et al. 1996). To analyze the effects of P availability on root exudation in tropical forests, the dynamics of organic acids were compared between a P-poor older soil (Spodosol) and a P-rich younger soil (Inceptisol) in the tropical montane rain forest of Mt. Kinabalu. The organic acid exudation from roots was found to be greater in the older soil than in the younger one (Fig. 2a), apparently a response to P deficiency. Accordingly, higher concentrations of organic acids were observed in the rhizosphere immediately surrounding roots in the P-poor soil (Fig. 2b; Fujii et al. 2012b).

Once organic acids are released into the rhizosphere, they are rapidly mineralized by microorganisms (van Hees et al. 2005; Fujii et al. 2010b, 2012b). This process may reduce the efficacy of organic acids on P mobilization (Jones et al. 2003). ^{14}C -tracer incubation experiments have shown that oxalate and citrate have short mean residence times in the rhizosphere (1–13 h; Fujii et al. 2012b). The high levels of low-molecular-weight organic acids in the rhizosphere could be maintained by greater root exudation in the older P-poor soil (Fig. 2a). The carbon (C) fluxes of organic acid exudation in P-poor soil represented 17 % of the aboveground NPP, which was greater than those in P-rich soil (3 %) (Aoki et al. 2012). By increasing the allocation of photosynthate to organic acid exudation in response to P deficiency, some tree species appeared to acquire P from the rhizosphere in P-poor soil in this Bornean tropical forest.

Fig. 2 Root exudation rates of organic acids (a) and organic acid concentrations in rhizosphere and bulk fractions (b) in the P-poor soil (Spodosol) and the P-rich soil (Inceptisol) of tropical montane forests in Mt. Kinabalu, Malaysia. Data and methods are from Aoki et al. (2012) and Fujii et al. (2012b)

Roles of ectomycorrhizal fungi in adaptation to acidic soils in tropical forests

Some symbiotic mycorrhizal fungi translocate nutrients directly from rock minerals to their host plants. These so-called “rock-eating fungi” are hypothesized to bypass P-deficient and Al-toxic soil conditions and competition against other microorganisms (Jongmans et al. 1997). A network of tubular pores (tunnels) is commonly observed in weatherable minerals in the surface layer of Spodosol soils under boreal coniferous forests (Fig. 3; van Schöll et al. 2008). Ectomycorrhizal roots can acquire P in association with mycorrhizal fungi that can solubilize weatherable minerals by releasing organic acids. In Bornean tropical forests, the growth-promoting effects of ectomycorrhizae (*Scleroderma* spp.) and the development of an ectomycorrhizal mat on an eluvial (white) layer of the acidic Ultisol soil were confirmed (Mori and Marjenah 2000; Fujii et al. 2011a). Nutrient mining by rock-eating fungi appears to be a common strategy for ectomycorrhizal tree species (Dipterocarpaceae, Fagaceae, and *Picea*), even in Bornean tropical forests (Taylor et al. 2009).

The ectomycorrhizal associations of dipterocarps have been considered one reason for their adaptation to the acidic soils of Southeast Asia. Dipterocarpaceae originated from the southern Gondwana supercontinent. They migrated via the movement of the Indian subcontinent, which split from eastern Gondwana in the Early Cretaceous and collided with the Eurasian plate 40–50 million years ago, then dispersed into Asia (out-of-India hypothesis) (Ashton 1982). The Dipterocarpaceae are hypothesized to have evolved the ability to associate with ectomycorrhizae specifically in Southeast Asia to acquire nutrients from acidic soils. Recently, the ectomycorrhizal association was reported to have originated before the India–Madagascar separation (Ducousso et al. 2004; Moyersoen 2006). Irrespective of the origin, Dipterocarpaceae can develop fine roots and

Fig. 3 Formation of the eluvial horizon underneath an ectomycorrhizal root mat of a tropical Ultisol soil (left) and tunnels in mineral grains formed by ectomycorrhiza fungi (right). The scanning electron microscopy picture of “rock-eating fungi” was taken with permission from van Schöll et al. (2008). Bar represents 10 mm

ectomycorrhizal systems in highly acidic soils in South-east Asia (Ashton 1988). The allocation of photosynthate to the roots or mycorrhizae contributes to the exudation of organic acids into the rhizosphere (Aoki et al. 2012). The finer ectomycorrhizal root systems facilitate organic acid exudation. The contemporary success of the Dipterocarpaceae, with high species diversity in Southeast Asia, is supported by their rhizosphere process of plant acquisition of P from highly acidic soils.

Regulation of organic matter decomposition by pH and lignin in tropical soils: importance of white-rot fungi to lignin degradation

The high nutrient demands of NPP in tropical forests can generally be met by rapid nutrient turnover in soils (Vitousek and Sanford 1986) via the rapid mineralization of organic matter by soil faunal and microbial activities in humid warm climates (Takeda 1998). On the other hand, the mechanisms of organic matter production and decomposition in the context of low soil pH and plant lignin richness can regulate efficient nutrient cycling in tropical forests by minimizing leaching losses, as discussed in the present and following sections.

Lignin is an important component regulating forest carbon and nutrient cycles because it provides persistent organic matter to soils (Salamanca et al. 1998; Osono 2007; Fujii et al. 2012c). Plants can defend themselves from herbivores by accumulating secondary metabolites such as lignin, tannin (proanthocyanidin), and alkaloids (Robinson 1990; Hättenschwiler and Vitousek 2000). Herbaceous plants can accumulate alkaloids or cyanogenic glycosides, whereas tree species can produce lignin-rich organic matter (ca. 30–50 % of plant dry weight). Although lignin production requires more energy (2.27 kJ g^{-1}) than cellulose production (1.74 kJ g^{-1}), tropical tree species can invest large amounts of photosynthate in lignin production to provide protection from herbivores and to increase stem strength (Robinson 1990). Based on the carbon/nutrient balance theory, allocating substantial photosynthate to lignin production may be an adaptive response to nutrient-deficient soil conditions in which C resources are “cheap” relative to the N resources needed to produce alkaloids (Bryant et al. 1983). This concept is consistent with the high lignin concentrations of dipterocarp litter in Bornean tropical forest on highly acidic soils (Fujii et al. 2009b).

Once organic matter is supplied to the soil, P and bases are released along with litter decomposition. Lignin degradation is a rate-limiting step for litter decomposition by microorganisms (Berg 2000; Wieder et al. 2009). During the early stages of decomposition, N and P can be immobilized through the fungal or abiotic formation of lignin-like humic substances associated with N and P (Anderson et al. 1983; Takeda 1995). During the latter stages of the decomposition process, N and P in these lignin-like humic substances are gradually

released as the lignin-like aromatic compounds are degraded (Berg and McLaugherty 1989; Osono and Takeda 2004). In some tropical-forest leaf litters, lignin-rich organic matter remains after the initial microbial attack (Fig. 4). These recalcitrant fractions accumulate as humified organic layers rich in N and P, but they turnover more rapidly than in temperate forests (Fujii et al. 2009b; Takeda 1998). In a Bornean tropical forest, the C/N ratio changed from 41 (fresh litter) to 24 (humified layer), while the C/P ratio changed from 1400 to 737. Assuming that the humified organic layer (43 % lignin) is decomposed with a mean residence time of 0.8 year (Fujii et al. 2009b), the annual loss of lignin ($2800 \text{ kg ha}^{-1} \text{ year}^{-1}$) can cause the stoichiometrical release of 80 and $2.6 \text{ kg P ha}^{-1} \text{ year}^{-1}$; these values are comparable to the litter production rates (99 and $3 \text{ kg P ha}^{-1} \text{ year}^{-1}$). Therefore, rapid turnover of lignin can be important to the high rates of nutrient supply from humic substances in Bornean tropical forests.

Lignin resists biological decay because its molecules consist of complex aromatic structures, it is insoluble and too large to pass through microbial cells, and lignin is degraded through oxidative reactions and cannot be cleaved by hydrolytic enzymes (e.g., cellulase) (Kirk 1984; Ten Have and Teunissen 2001). Only white-rot basidiomycete fungi can decompose lignin effectively by secreting enzymes such as lignin peroxidase (LiP) and manganese peroxidase (MnP) (Hatakka 2001; Hofrichter 2002). The development of these ligninolytic enzyme systems in basidiomycetes arose 290 million years ago and might have led to the sharp decrease in the rate of organic C burial (as evidenced by the formation of coal deposits derived primarily from lignin) at the end of the Carboniferous period (Floudas et al. 2012).

Lignin degradation exhibits higher temperature-dependency than cellulose degradation (Donnelly et al. 1990), and lignin is more rapidly degraded in tropical regions than in temperate ones, where cellulose is

Fig. 4 Lignin leaf skeleton of *Dipterocarpus cornutus* in tropical forest. Lignin-rich veins remain after initial microbial attack

selectively decomposed over lignin (Takeda and Abe 2001). White-rot fungi and their enzymes (LiP and MnP) play major roles in the rapid lignin degradation in tropical forests (Osono et al. 2009; Fujii et al. 2012c). In acidic soils, total microbial activity and cellulose decomposition are generally restricted (Fig. 5a), while LiP can exhibit high redox potential under acidic conditions, resulting in high rates of lignin degradation (Fig. 5b; Kirk et al. 1978; Marquez et al. 1988). A decrease in pH in the forest floor layers, along with an increase in fungal activity, results in a shift in ligninolytic enzyme activity toward the dominance of LiP in the humified organic layers (Fig. 5b). LiP has evolved and adapted to acidic conditions to enable the effective oxidation of non-phenolic lignin, which requires a high redox potential for degradation (Marquez et al. 1988; Oyadomari et al. 2003). LiP, which can be produced only by Polyporales basidiomycete fungi (Morgenstern et al. 2008), solubilizes recalcitrant lignin and releases nutrients and aromatic substances into the soil solution (Reid et al. 1982). The adaptation of fungi to acidic and lignin-rich environments results in the rapid degradation of organic matter and meets the high demand for nutrients in the acidic soils of Bornean tropical forests.

Roles of dissolved organic matter in the N, P, and base cycles in tropical forests

In forest ecosystems, most of the organic matter supplied to the organic layer mineralizes to CO₂, but a

proportion (~30 %) is leached as dissolved organic matter (DOM) as soil water percolates (McDowell and Likens 1988). DOM is an intermediate by-product of litter decomposition by microorganisms. Because low-molecular-weight organic acids and sugars [$<10\%$ of the dissolved organic C (DOC)] released from fresh litter and roots are mineralized to CO₂ within hours (Fujii et al. 2010b), the dominant DOM fractions leached from the organic layer are recalcitrant high-molecular-weight humic substances (Guggenberger and Zech 1994; Qualls and Bridgman 2005). DOM may play important roles in the cycling of basic cations, N, and P within forest ecosystems (Qualls et al. 1991; Schwendenmann and Veldkamp 2005; Fujii et al. 2013b).

The formation of thick organic layers has typically been considered to lead to a sizable production of DOM in cool and humid climates (Michalzik et al. 2001). Conversely, in tropical forests, the rapid mineralization of litter to CO₂ has been hypothesized to result in low concentrations of DOM in soil solutions (Johnson 1977). However, in some of the tropical forests of East Kalimantan, a large flux of DOM is released from the thin organic layer (Fig. 6; Fujii et al. 2009b, 2011c). Data synthesis indicated that large DOC fluxes from the organic layer in tropical forests can be caused by high precipitation and C input (sum of throughfall and litterfall) (Michalzik et al. 2001; Fujii et al. 2009b). The proportion of DOC flux relative to C input increased with decreasing pH (Fig. 7a), suggesting that the sizable production of DOC in the organic layer is common to acidic soils (pH <4.3) in both temperate and tropical forests (Fujii et al. 2009b). The larger DOC flux at lower pH results from the release of aromatic compounds via lignin solubilization (Guggenberger and Zech 1993; Fujii

Fig. 5 Relationships between soil pH and cellulolytic activity (a) and lignin peroxidase (LiP) activity (b). Bars indicate standard errors. Data for cellulolytic and LiP activities from Fujii et al. (2012c) and Hayakawa (2013), respectively

Fig. 7 Relationships between soil pH and dissolved organic carbon (DOC) leaching from the organic layer (a) and foliar P concentrations and DOC concentrations in the organic layer leachate in five Indonesian forests (b). The DOC leaching was calculated as the proportion of DOC flux from the organic layer relative to C input (throughfall-DOC and litterfall-C). Data from Fujii et al. (2009b, 2011c)

et al. 2011b), which is enhanced by the high activity of fungal enzymes (LiP; Fig. 5b). Within the five tropical forests in East Kalimantan, the magnitude of DOC leaching from the organic layer increased with decreasing P concentrations in the foliar litter (Fig. 7b; Fujii et al. 2011c). Low P concentrations in the foliar litter, as well as a high lignin concentration, could reduce DOC biodegradability and increase DOC leaching from the organic layer (Wieder et al. 2008).

DOM can transport basic cations (Fig. 1) and N and P in organic form (Fig. 6). Because DOM leached from the organic layer is stabilized by sorption onto clays (Sollins et al. 1996), leaching loss from the soil is minimal (Fig. 6). Once DOM is stabilized in the mineral soil layers, soil organic matter functions as a reservoir and slow-release source of N, P, and bases (Kalbitz et al. 2000). The production of tannin-rich litter is hypothesized to be an adaptive strategy of coniferous trees for minimizing the leaching loss of N from nutrient-limited forests (Northup et al. 1995a, b). In nutrient-limited Bornean tropical forests, DOM-driven nutrient cycles can increase P solubility in the surface soil layer through the competition for sorption sites by organic anions and can minimize loss of dissolved organic P through sorption in the subsoil. Considering that development of efficient nutrient cycles through carbonic acid leaching has also been reported for the less acidic soils of tropical forests in Central America (Johnson 1977), there might exist two different mechanisms that drive tight nutrient cycling within tropical forests. Bornean tropical forests on highly acidic soils appear to develop DOM (or organic acid)-driven nutrient cycling to acquire bases and P and minimize their losses.

Why can Bornean tropical forests maintain high productivity or diversity on highly acidic soils?

Soil acidification driven by plants and microorganisms does not simply mean “soil degradation” in Bornean tropical forests. Rather, this process reflects mineral weathering induced by plants and microorganisms and their acquisition of soil nutrients. Plant productivity is

not dependent solely on static factors of climate and soil nutrient levels (Terborgh 1992). The high biomass production by tropical trees is supported by the adaptations of plants and microorganisms to an acidic soil environment. Root exudation of organic acids can increase in response to P deficiency as well as Al toxicity in acidic soils and can mobilize P in the rhizosphere. The decomposition of organic matter can also be promoted by increased fungal activity at low pH. The specific enzyme produced by white-rot fungi (LiP), which can exhibit lower pH optima than other enzymes, increases lignin solubilization and the production of DOM. These findings can account for the adaption and success of Dipterocarpaceae in the acidic soils of Southeast Asia. In contrast to the dominance of fast-growing species and the exclusion of slow-growing ones on nutrient-rich soils, slow-growing Dipterocarpaceae can exhibit high species richness by acquiring tolerance to acidic soil environments (Baillie et al. 1987; Ashton 1988; Paoli et al. 2006). In addition to ectomycorrhizal associations and root exudation, the indirect effects on fungal activity and DOM production contribute to the acquisition of nutrients without the leaching losses observed in cropland soils due to the imbalance between nitrification and plant uptake (Fujii et al. 2009a).

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