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Biodegradation of low molecular weight organic acids in rhizosphere soils from a tropical montane rain forest

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ABSTRACT

Root exudation of organic acids could be an important strategy for plant acquisition of phosphorus (P) from P-deficient soils in tropical rain forests. However, the efficacy of organic acids on P mobilization in the rhizosphere could be reduced due to their rapid biodegradation by rhizosphere microorganisms. To assess the dynamics and function of organic acids in the rhizosphere soils in tropical rain forests, we examined the concentrations of oxalate, citrate, and malate in soil solution and the mineralization kinetics of ^{14}C-radio-labelled oxalate and citrate in the rhizosphere and bulk soil fractions. We compared two tropical montane rain forests from Mt. Kinabalu, Borneo that share similar parent material (i.e., sedimentary rocks) and climate but differ in terms of soil age. The older soil (Tertiary age materials) was affected by podzolization and had less inorganic labile P compared to the younger soil (Quaternary colluvial deposits). In the P-deficient older soil, the rhizosphere soil solution contained markedly higher concentrations of oxalate, citrate, and malate than did the bulk soil, whereas in the P-rich younger soil, the levels of organic acids in the rhizosphere were lower. The higher levels of organic acids in the rhizosphere of P-deficient soils are caused by greater root exudation and the lower sorption capacity for organic acids. The results of mineralization kinetics showed that oxalate and citrate in soil solution were rapidly mineralized in both rhizosphere and bulk fractions of both P-rich and P-deficient soils, having short mean residence times (2.3–13.1 h for oxalate and 0.8–1.6 h for citrate). The mineralization rates of oxalate and citrate were highest in the rhizosphere fraction of the P-deficient soil, where the pool of organic acids was largest and rapidly replenished by root exudation. Our data indicate that consumption as well as production of organic acids in the rhizosphere could be enhanced in P-deficient soil. The efficacy of organic acids on P mobilization in the rhizosphere in tropical montane rain forests appears to vary depending on the level of soil P availability and the anion sorption capacity, attributable to soil aging with podzolization.

1. Introduction

In the humid tropics, long-term weathering of soils generally results in a decrease in phosphorus (P) availability (Walker and Syers, 1976). The P deficiency caused by this process can eventually limit biomass production (Wardle et al., 2004). In Borneo, however, tropical rain forests can maintain massive biomass production and biodiversity on highly weathered soils (Kitayama et al., 2004; Kitayama, 2005). Several adaptive mechanisms to P limitation have been reported: the tight recycling of P through ectomycorrhizal and fine root systems (Jordan and Herrera, 1981; Lambers et al., 2008), the higher P utilization efficiencies of plants (Kitayama et al., 2004), and the use of non-labile P through root exudation of organic acids and enzymes (i.e., phosphatase) (Treseder and Vitousek, 2001; Liu et al., 2006).

Because the di- and tri-carboxylic acids can solubilize recalcitrant P bonded with aluminum or iron oxides and enhance P concentrations in rhizosphere soil solutions (Gardner et al., 1983), root exudation of organic acids could be an important strategy for plants to acquire P in the P-deficient soils in tropical rain forests. Some plant species can exude particular organic acids as a result of long-term adaptation to P-limited soils (Ström et al., 1994; Grayston et al., 1996; Zhang et al., 1997). Root exudation of organic acids, mainly oxalic, citric, and malic acids, from these plants has been shown to be greatly enhanced in response to P deficiency (Gardner et al., 1983; Ström et al., 1994; Jones, 1998). Although the concentration of low molecular weight organic acids (LMWOAs) is generally low in soil

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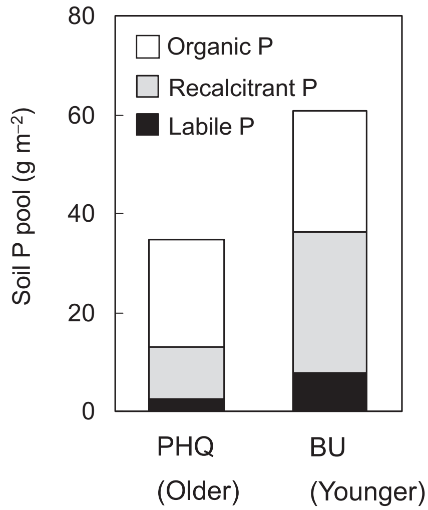

Fig. 1. Soil P fractions in the profiles. Data were expressed on an area basis (0–30 cm). Labile P includes inorganic P fractions extracted by $NaHCO_3$, NaOH and HCl from soil. Residual P is termed as recalcitrant P. Organic P is sum of organic fractions extracted by $NaHCO_3$, NaOH and HCl from soil. The data source is Kitayama et al. (2004).

solution (Strobel, 2001; Van Hees et al., 2002), rhizosphere soils may contain locally high concentrations of LMWOAs (Jones et al., 2004; Sandnes et al., 2005). In tropical rain forests, root exudation of organic acids in the P-deficient older soil is hypothesized to be greater than in the P-rich younger soil, and this may contribute to the higher levels of organic acids in the rhizosphere of P-deficient older soil.

On the other hand, LMWOAs in soil solution are easily biodegradable, having short mean residence time (MRT) in topsoil ranging from 1 to 6 h in temperate regions (Jones et al., 1996; Van Hees et al., 2005a). Biodegradation by rhizosphere microorganisms has been shown to reduce the ability of organic acids to mobilize P (Jones et al., 1996; Ström et al., 2001; Hashimoto, 2007). Because microbial activity generally increases with temperature and it may be enhanced in the rhizosphere (Ström et al., 2001; Hayakawa et al., 2011), biodegradation of LMWOAs may also be faster in rhizosphere soils of tropical rain forests than in temperate soils. The rapid biodegradation of organic acids might reduce the ability of organic acids to mobilize P in tropical rain forests. However, the efficacy of organic acids in the rhizosphere of P-deficient soils is still unclear due to limited knowledge about biodegradation of organic acids in tropical rain forests.

To investigate the role of organic acids on P mobilization in the rhizosphere of tropical rain forest soils, we tested (1) whether the concentration of organic acids was enhanced in the rhizosphere of P-deficient soil. Oxalate, citrate, and malate are the dominant organic acids exuded from roots in response to P deficiency (Jones, 1998) and thus were selected for this study. We also tested (2) whether biodegradation of organic acids was enhanced in the rhizosphere of P-deficient soil. Of the three organic acids, oxalate and citrate were selected for the biodegradation studies because they are both common and play an important role in P mobilization in soils (Ström et al., 2002; Jones et al., 2003). In particular, oxalate exhibits the greatest sorption and the lowest biodegradability of the three (Jones and Brassington, 1998; Ström et al., 2001; Fujii et al., 2010).

2. Materials and methods

2.1. Site description

On southern slopes of Mount Kinabalu (6°05′N, 116°33′E, 4095 m a.s.l.), Sabah, Malaysia, we compared two tropical montane rain forests at Park Headquarters (PHQ) and Bukit Ular (BU), which shared similar parent material (i.e., sedimentary rocks) and climate but differed in terms of soil age (Table 1). The PHQ soils were derived from Tertiary sedimentary rocks, consisting of sandstone and mudstone of the Eocene Trusmadi Formation, and were affected by podzolization. The BU soils were derived from colluvial deposits that were passed down from upper elevations in the Quaternary period (30,000–40,000 yrs ago). Podzolization resulted in a decrease in soil pH, clay content, and amorphous Fe and Al (hydr)oxides in the surface PHQ soil compared to BU soil (Table 2). According to Hedley sequential P fractionation, the older PHQ soil had less total and available P compared to the younger BU soil (Fig. 1) (Kitayama et al., 2004). The tree genera *Lithocarpus* (Fagaceae) and *Syzygium* (Myrtaceae) dominated the BU site, whereas the site-specific genera *Tristaniopsis* (Myrtaceae) and coniferous *Dacrycarpus* and *Dacrydium* (Podocarpaceae) were abundant at the PHQ site.

2.2. Soil sampling

The soil samples were collected from five pits at both sites in August 2010. The distance between each pit was 10 m. The surface mineral soil horizons (0–10 cm), where the activities of roots and microorganisms and the P dissolution reaction are considered to be high, were collected and analyzed (Table 1). The fresh, unsieved soil samples were separated into rhizosphere and bulk fractions following the method by Wang and Zabowski (1998). Rhizosphere soil was obtained by gently shaking the fine root systems (<2 mm) approximately 10 times until the loosely adherent soil was removed and then by carefully scraping the roots to collect closely adhering soil. The bulk fraction was collected from the soil outside the rooting area. Both soil fractions were used for soil solution extraction, sorption, and mineralization kinetic studies. After removing rhizosphere soil, roots were washed and scanned in a flat screen scanner (GT-S600, EPSON, Tokyo, Japan), and the root surface area was analyzed using Win-Rhizo (Regents Instruments Inc., Quebec, Canada). The thickness of the rhizosphere soil was calculated by

Table 1
Site description.

Site	PHQ (Older soil)	BU (younger soil)
Elevation (m)	1560	1860
Annual mean precipitation (mm yr^{-1})	2380	2380
Annual mean temperature (°C)	18	18
Dominant vegetation[a]	*Syzygium* sp., *Tristaniopsis* sp.	*Syzygium* sp.
	Lithocarpus clementianus	*Lithocarpus* sp.
	Dacrycarpus imbricatus	*Castanopsis kinabluensis*
Aboveground biomass (kg m^{-2})	28.0	35.2
Parent material	Sedimentary rock[b] (Tertiary age materials)	Sedimentary rock[b] (Quaternary colluvial deposits)
Soil type[c]	Spodosols	Inceptisols

[a] The list of vegetation genus was given in Aiba and Kitayama (1999) and Kitayama et al. (2004).
[b] The sedimantary rocks consist of sandstone and mudstone of the Eocene Trusmadi Formation and generally contain more than 50% quartz (Jacobson, 1970).
[c] Soil types were classified based on Soil Taxonomy (Soil Survey Staff, 2006).