

Phosphorus Biogeochemical Cycle Research in Mountainous Ecosystems

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Abstract: Phosphorus (P), as a limiting nutrient, plays a crucial role in the mountainous ecosystem development. Its biogeochemical cycle in mountainous ecosystems determines the bioavailability and sustainable supply of P, and thus becomes a crucial process which needs to be fully understood and described for ecological and environmental conservation. However, most of research about P biogeochemical processes has been carried out in aquatic environment and agronomic field, but rare researches have been done in mountain ecosystem. In the present review, we summarize researches on P biogeochemical cycle concerning mountain ecosystem in recent decades, including rock weathering, the release, transformation and bioavailability of P, interactions between the P biological cycle and microbial and plant life, as well as the development of models. Based on the state of art, we propose the future work on this direction, including the integration of all these research, the development of a practical model to understand the P biogeochemical cycle and its bioavailability, and to provide a reference for ecological and environmental conservation of mountainous ecosystems and lowland aquatic systems.

Keywords: Phosphorus; Biogeochemical cycle; Weathering; Microbe and plant; Model; Mountainous ecosystem

Introduction

Phosphorus (P) is one of the essential

elements for plant growth (Filippelli 2008; Tiessen et al. 2011). It is a major component in organic compounds in plants, takes part in plant physiological and biochemical processes and plays a vital role in plant growth. According to biostochiometric theory, there is an equilibrium ratio among nutrients for healthy ecosystem development (Sturner and Elser 2002). This equilibrium will be broken if one nutrient is insufficient or in excess, which may affect the eco-process and the primary productivity. In this case the element concerned is considered as the limiting nutrient for the ecosystem development. In the terrestrial ecosystem, nitrogen (N) and P are two most common limiting elements. In young soils, N is the major limiting element due to its shortage, while P becomes the major limiting element in the long-term developed soils due to its continuous depletion (Walker and Syers 1976; Vitousek et al. 2010). In contrast to N which is mainly from atmospheric deposition (Galloway et al. 2004), the source of P in ecosystems is significantly from rock weathering (Walker and Syers 1976). Compared with N, the P cycle in the pedosphere and biosphere is a relatively closed and slow process (Smil 2000), while its bioavailability plays a vital role in the absorption and assimilation of N by plants (Crews et al. 2000). On the other hand, the increasing N deposition, a significant feature of global change (Tian et al. 2010), is apt to result in P limitation (Vitousek et al. 2010). Therefore, in most ecosystems, especially in the terrestrial ecosystem, P would become the ultimate limiting nutrient

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(Tiessen 2008). Concerning P biogeochemical cycle and its effect on ecosystem, a lot of researches has been done in aquatic and agronomic ecosystem. Mountainous ecosystems represent a typical terrestrial ecosystem, where the steep slope and thin soil layer cause easy loss and insufficient supply of P. Recent research has demonstrated that P became the major limiting element in some mountainous and high latitude ecosystems instead of N (Bowman 1994; Seastedt and Vaccaro 2001; Wassen et al. 2005).

Lots of researches have demonstrated that the distribution of vegetation zone, especially the vertical distribution pattern in mountainous areas, is controlled by climatic condition. The growth limit of species, such as the tree line, is controlled by temperature (Korner 1998). However, as pointed out by Sala et al. (2000), climate change might not be the only factor impacting the ecosystem development. Biogeochemical cycle and bioavailability of nutrients should not be neglected. At the retreated area of the Hailuoguo Glacier in Gongga Mountain, Southwest China, within a ca. 2 km long distance and an altitude from ca. 2,900 m a.s.l. (above sea level) to 3,000 m a.s.l., the primary vegetation succession has developed, which can be described as five clear belts according to their dominant species: bare land - herds; *Salix-Hippophae-Populus*; *Populus*; *Picea, Abies-Betula-Rhododendron*; and *Picea-Abies* (Zhong et al. 1999; Li and Xiong 1995). How does the primary succession develop at this altitude where *Picea* should be the dominant species? The climate has not large difference within such a limited area. Studies indicated that at the glacial retreated area, P and N were both limiting elements for developing vegetation at the beginning of the pedogenic process due to the lack of N in mother rocks and scarcely available P from weak weathering and immature pedogenesis. Although the amount of available P is limited, it is possible to meet the demand for microbial development. Microbes assimilate atmospheric carbon (C) and N, excrete acid and enzymes which promote weathering and P release, and increase the availability of P. Therefore, in the retreated area, the pioneer plant is the species with the function of N fixation, such as *Astragalus mongholicus*. As P availability increases, some higher plants emerge and then the vegetation primary succession is developed (Data

submitted to Geoderma).

Since atmospherically deposited particles bring limited amounts of P into the terrestrial ecosystem (Filippelli 2008), the major source of P is from rock weathering. The global P cycle at a relatively short time scale can be regarded as a unidirectional process of discharge from weathering terrains and accumulation in the ocean (Vitousek et al. 2010). Therefore, the loss of P from the terrestrial ecosystem, even a very small amount, is difficult to recover under natural conditions. Research has indicated that the long-term P loss causes ecosystem retrogression in the long developed and highly weathered soils of wet tropical and subtropical areas, as well as high sand content soils from semi-arid tropical areas (Crews et al. 1995; Kitayama and Aiba 2002; Richardson et al. 2004; Selmants and Hart 2010; Wardle et al. 2004). Some studies in Europe and North America demonstrated that the increased N deposition caused acidification of forest soils, and then changed the bioavailability of P. As a result, forest ecosystems were faced with gradual retrogression and biodiversity loss (De Schrijver et al. 2011; Roem et al. 2002).

The terrestrial ecosystem is a P source, while the water ecosystem is a sink of P. Excess P discharge into the water is the major factor causing eutrophication (Smith 2003). Mountains are the most significant material source area and the beginning of global material and energy cycling, and play a crucial role in the global mass and energy balance (Raymo et al. 1988). Therefore, fluxes and bioavailability of P exported from mountains directly affect the lowland water quality.

Mountain is a major landform unit which covers a large part of the terrestrial area. For instance, mountains cover nearly 70% of land area in China. Mountains, especially the high altitude areas are more sensitive to global changes than other landforms. They are always steep, and thus have sharp altitude gradients of climate, hydrology and also nutrients. Meanwhile, mountain areas are places with abundant biodiversity and vulnerable ecosystem. As mentioned above, the biogeochemical cycle of P controls its bioavailability, allocation and transportation in the mountain ecosystem. Therefore, research on the biogeochemical cycle of P in the mountain ecosystem deserves more attention whether from

the view point of development and security of mountain ecosystem or of eco-environment security of lowland water systems.

In this review, we summarize the current researches on P biogeochemical cycle in the mountain ecosystem including the rock weathering, mechanisms of the release, transformation and bioavailability of P in soils, interactions between P biogeochemical cycle and microbial and plant life, as well as the development of P models.

1 General Characteristics of P Biogeochemical Cycle in Mountain Ecosystems

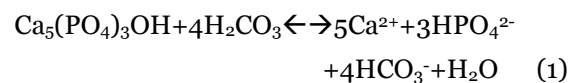
As a unique terrestrial geomorphologic unit, the biogeochemical cycle of P in mountains follows the same basic processes as in other terrestrial ecosystems (Figure 1) (Buendia et al. 2010). P is released from rocks (mainly apatites) by weathering. Some released P, being readily bioavailable, can be incorporated into plant tissues or assimilated by microbes and then converted into organic forms. Some released P is either co-precipitated with secondary minerals (iron (Fe), manganese (Mn) and aluminum (Al) oxyhydroxides) or adsorbed onto their surfaces which cannot be directly utilized by plants and microbes. Under the change of conditions, such as pH, temperature and redox potential (Eh), this kind of P may be transformed to bioavailable fractions. The rest of P released will be transported downwards and ultimately lost from soils by runoff or leaching. With the death and decay of plants and tissues, P contained in the biomass is returned to soils and converted into either bioavailable forms or occluded forms by decomposition and mineralization. The atmospheric deposition of P accounts for a small part of its content in most terrestrial ecosystems, while the main source of P is rock weathering (Filippelli 2008).

The P biogeochemical cycle in the mountain ecosystem, especially alpine ecosystems, has its unique characteristics due to the vertical zonality. The remarkable characteristics of the P biogeochemical cycle in the mountain ecosystem include: 1) runoff which plays a crucial role in P transportation and results in quick P loss from mountainous soils due to the large elevation

difference and steep slope; 2) the P sub-cycle (from lithosphere to biosphere and then back to the pedosphere) which is heterogeneous due to the different land covers and zonalities of vegetation and soils; 3) a large portion of P stored in biomass due to higher forest primary productivity; and 4) the decomposition and mineralization of litter which provide a significant replenishment of the bioavailable P pools in soils.

2 Mechanisms of P Release by Weathering and Evaluation of Release Rate

Atmospheric CO₂ dissolved in water forms weak carbonic acid which, together with the acid released by plant roots and microbes through biochemical respiration, attacks P-bearing minerals (generally apatites) (Formula 1). This is referred to as P-bearing rock weathering. Thereafter, P is released from the rock (Schlesinger 1997) as shown in the following equation:



Weathering is influenced by several environmental and biological factors. The environmental factors include temperature, precipitation, pH, Eh and so on. The biological factors include the changes of pH and Eh induced by plant and microbial respiration and secretion, and chelation reactions induced by organic acids (Harley and Gilkes 2000). A study at a glacial-interglacial time scale indicated that the global dissolved P flux possibly increased 40%-45% during the first hundred years of the deglaciation phase due to the increasing soil humidity and runoff induced by glacier melting with the increased temperature (Föllmi et al. 2009). The weathering rate in forests was triple that in the bare area in the Rocky Mountain National Park, Colorado (Arthur and Fahey 1993). Other research carried out in North and South America indicated that the chemical weathering rate in areas with vegetation was 4 to 5 times higher than that in areas without vegetation (Benedetti et al. 1994; Taylor and Velbel 1991).

Many studies have been designed to establish a quantitative relationship between the rock

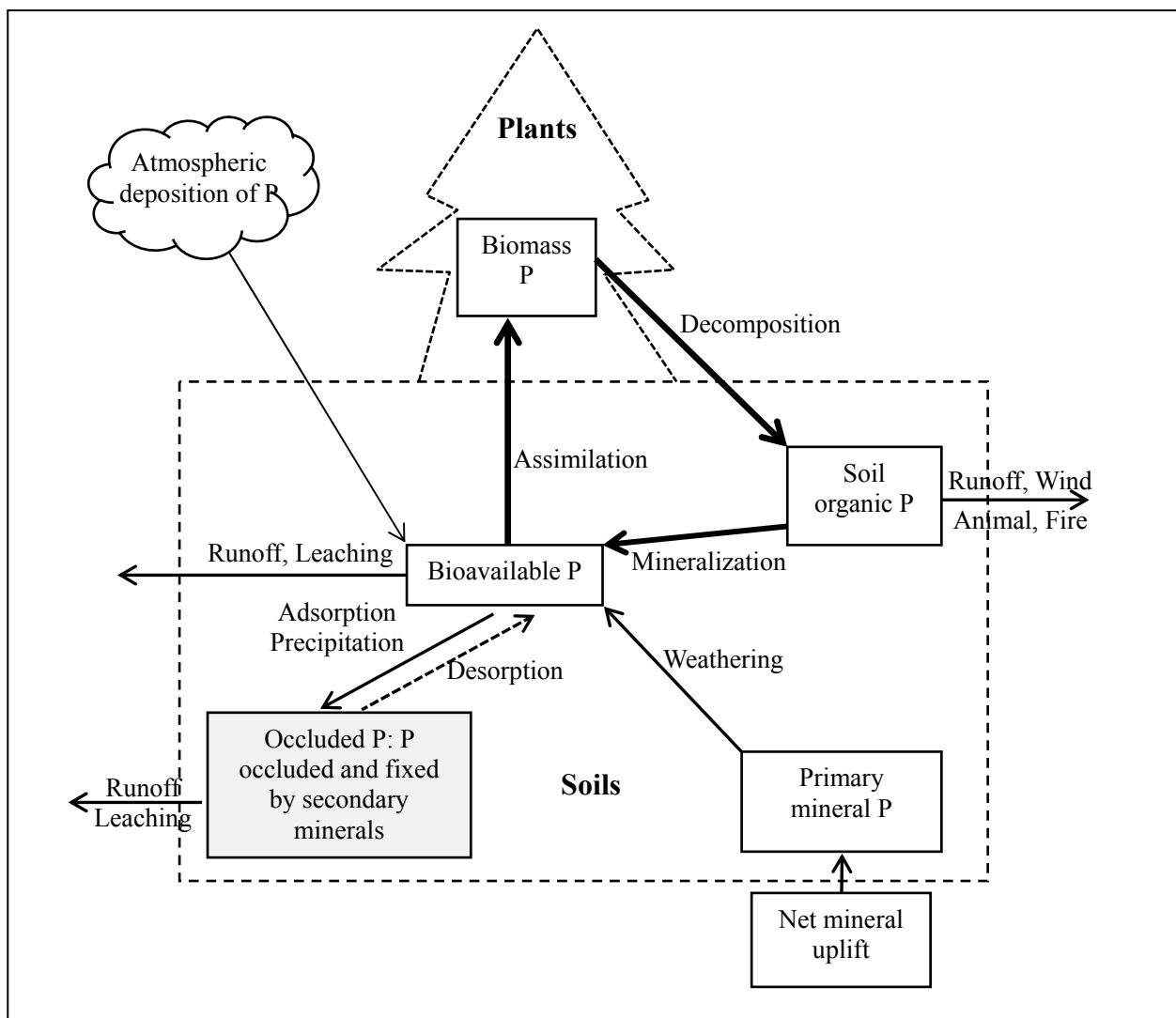


Figure 1 Schematic representation of the terrestrial P cycle (modified from Buendia et al. 2010)

weathering and the P release rate. However, weathering is a time consuming process, which is difficult to directly measure the weathering rate and P release rate in the field or laboratory. Gardner (1990), based on the isovolumetric geochemical analysis, estimated the P release rate using the export of dissolved silica (Si) in rivers, assuming that dissolved P and Si released from rocks undergo weathering in the same proportion as that in the fresh rock. However, there are two major limitations in Gardner’s method. A relatively large error might have resulted from varied lithology and different weather conditions in a relatively large watershed. Moreover, his method did not consider interactions between the weathered rocks and the upper soil layers. Fillpelli and Souch (1999) suggested that the ratio of

germanium to Si (Ge/Si) was more suitable to estimate the P release from rocks in regions where chemical weathering was low (for example, in the alpine area), since compared to Si, Ge appeared to be preferentially fractionated in the solid phase in low chemical weathering regimes, and then transported to the dissolved phase in areas of intense weathering (Filippelli and Souch 1999). This method can be applied at the watershed scale and glacial-interglacial time scale, while a proper sediment core is required to obtain Ge/Si data. Walker and Syers (1976), based on four chronosequences in New Zealand, evaluated the P weathering rate on the same parent materials indicating that P released by weathering could be calculated from the decrease in total P and the increase of organic P (Newman 1995). Thereafter,

many studies have similarly used chronosequences to predict P loss by weathering (Turner et al. 2007; Eger et al. 2011; Poder and Hilley 2011). A model, proposed by Hartmann and Moodsdorf (2011), combined the factors of spatial heterogeneity (such as lithography, runoff, slope, and land cover) with hydrochemical data, was used to precisely calculate the P release rate at a watershed scale. It can also be used to distinguish the most significant factors that control chemical weathering. The results showed that lithology and runoff were two major factors controlling the chemical weathering rates.

3 Physiochemical Processes of P in Soils

The transportation and transformation of P in soils are the result of a series of physiochemical processes such as adsorption-desorption, precipitation, complexation, leaching, loss from runoff and so on (Sparks 2003). These processes are influenced directly or indirectly from temperature, moisture, parent rocks, microtopography, biological effects and global changes (such as climate change, acid deposition, etc.). Higher soil temperature and moisture, less clay contents, and steeper slope cause less bioavailable P to be adsorbed onto secondary mineral surfaces, and increase the content of bioavailable P in soils (Runyan and D'Odorico 2012). Meanwhile, these conditions also induce an increase in P loss. For example, the soil moisture changes soil Eh, which is one of the controlling factors fundamentally affecting the secondary mineral P pools through transformations of Fe fractions (Turrion et al. 2008). Organic acid excreted by plants and microbes can decrease soil pH which also changes Al and Fe fractions, and thus increases P bioavailability in soils (Ohno et al. 2007).

A study in the Hawaiian montane forest soils indicated that redox conditions controlled P pools (Miller et al. 2001). The results demonstrated that the organic P pools increased, while the inorganic P pools decreased with the decreased Eh which was induced by increasing rainfalls. The total P in the soils declined nearly 2/3 because of increasing rainfall and reducing conditions. Another research found that the P loss was positively correlated with

the ionic Fe loss due to decreased Eh (Devau et al. 2009). In addition, in the European alpine ecosystems, Al oxyhydroxides were the major controlling factor for the soils to retain phosphate (Kana et al. 2011).

Bioavailable P is mainly adsorbed by Fe oxides, gibbsite and clay minerals when the soil is acidic, alkaline and neutral, respectively (Devau et al. 2009). Therefore, the impact of pH on P retention and bio-availability in soils can be attributed to its effect on Al and Fe oxides. For instance, a decrease of pH can increase the mobility of Al hydroxides and the solubility of primary mineral P, and then release bioavailable P contained to soils (Ohno and Amirbahman 2010). Atmospheric deposition of N and sulfur (S) may cause the soil acidification, and also change the P retention capability of soils (Sherman et al. 2006). Additionally, it is also found that P bioavailability in the soil layers of 0-80 cm significantly increase after an application of 120 kg ha⁻¹ of S-SO₄ (Skwierawska and Zawartka 2009).

The uneven vertical allocation of soil P is the result of water conditions, lithology of parent rocks and biological processes (Brady and Weil 2007). There is an argument over which factor controls the vertical heterogeneity of P allocation. Some researchers indicated that the plant uptake was the major factor controlling P vertical allocation in soils (Ippolito et al. 2010; Jobbagy and Jackson 2004). However, others concluded that it was the water cycle in soil profiles that control the P allocation (Porder and Chadwick 2009). A recent study in the Gongga Mountain, Southwest China, indicates that the effect of plant uptake on P allocation increases with the decreasing elevation (Unpublished data).

The soil age plays a vital role in the soil P fractionation, transformation and loss (Walker and Syers 1976; Turner et al., 2007; Selmants and Hart 2010; Eger et al. 2011). Walker and Syers (1976) suggested that the stock of P in parent materials would become exhausted and P would be gradually depleted from the ecosystems through erosion and leaching, and then the geochemically “occluded” P pools would increase with the soil development. However, another study showed that it was the leaching rate and secondary minerals which determine the P pools and its bioavailability rather than the age of soil development (Porder and Hilley 2011).

4 Biological Processes of P Biogeochemical Cycle in Mountain Ecosystems

4.1 Interaction between P biogeochemical processes and microbes

Microbes are involved in the P biogeochemical cycle through weathering, litter decomposition, mineralization and mobilization of non-labile phosphate. One of the microbial effects on the P biogeochemical cycle is the increase of P bioavailability in soils. Microbes release organic and/or inorganic acids into soils and other metabolites. As a result, the soil pH is changed and Al or Ca chelates are formed, which can accelerate weathering and block the formation of insoluble phosphate (Lian et al. 2008).

Microbial mass P itself, which constitutes 20%-30% of total organic P in soils, is an important source of bioavailable P (Tate 1988). Microbes increase the bioavailability of P in soils, and thus promote the P uptake ability of plants. Research on *Arbuscular mycorrhiza* fungi (AMF) shows that the AMF's improvement effect can be demonstrated by three aspects: (a) AMF obtains carbohydrate from plants, and in turn supplies P for plants. When AMF colonizes plant roots and forms the symbiosis, lateral hyphae grow from roots into soils. The hyphae increase the length and surface area of roots. (b) Faster movement of P into mycorrhizal hyphae is achieved by increasing the affinity for P ions and by decreasing the threshold concentration required for the absorption of P. (c) Solubilization of soil P is based on the release of organic acids and phosphatase enzymes (Bolan 1991; Olander and Vitousek 2004; Richardson and Simpson 2011). The exception is that AMF competes for P with plants when microbial mass C/P ratios are high (Joner et al. 2000). Acid and/or alkaline phosphatase secreted by microbes play an important role in the hydrolysis of organic P (Hagerberg et al. 2003; Nilsson and Wallander 2003).

Environmental factors affect microbial functions in the P biogeochemical cycle. The organic matter content, temperature, soil moisture and other conditions control the P mineralization rate by microbes. Schmidt et al. (1999) found that

the net P mineralization and immobilization were higher in the heath soil than in the transplanted fell field soil. The likely interpretation for this observation is that a larger part of labile P in the fell field soil is not fixed in the microbial biomass but bound with minerals. Grierson et al. (1999) found an increase in water potential from -10 kPa to -0.1 kPa, which induced KCl-extractable inorganic P concentrations increased between 38% and 239%, and this depended on the incubation temperature and time. An increase in incubation temperature from 15°C to 38°C increased the KCl-extractable inorganic P concentrations between 13% and 53%. The impact of soil temperature and moisture on microbial activity is involved in the decomposition rate of litter and humus, the mortality rate of microbes, the plant P demand, and leaching of P from the rooting zone. High soil moisture stimulates humus decomposition and leaching, and thus accelerates P mineralization. Some researchers reported that Al oxides affected microbial activity in the P transformation (Runyan and D'odorico 2012; Grierson et al. 1999). High Al oxide contents probably induced the stabilization of soil organic compounds, and then reduced microbiological activity and mineralization rates (Achat et al. 2012).

It is well known that the development and activity of microbes are mainly limited by C and N in natural ecosystems. Microbes are also influenced from other nutrients (especially P) during C sequestration. Some reports showed that the ectomycorrhizal fungi productivity is stimulated by apatite addition in the forest soils containing low P, while there is no significant effect in the abundant P soils (Hagerberg et al. 2003; Nilsson and Wallander 2003). Whether P is a limiting nutrient for microbe development is usually observed by the response of microbes to P application. Research showed that when the bioavailable P content was lower than 34 mg kg⁻¹, the growth of AMF was negatively correlated with the bioavailable P content in soils. This indicated that the lower the content of soil bioavailable P, the more the roots increase AMF activity and promote P transformation. Liu et al. (2012) found that microbial biomass significantly increased, and the microbial community was changed due to a long-term high N deposition and the shortage of P.

4.2 Interaction between P biogeochemical processes and plants

Other than N, P is regarded as the second most limiting nutrient in many ecosystems for plant growth (Soudzilovskaia et al. 2005; Vitousek et al. 2010). As an essential component of plant cells, P is one of the key elements in enzymes responsible for energy storage and transformation, and thus its deficiency may threaten plant cell integrity (Giesler et al. 2012). Research has also indicated that the P shortage may decrease the growth rate, aboveground biomass, nutrient concentration and photosynthetic capacity of plants (Tinker and Nye 2000; Vance et al. 2003; Hill et al. 2006). However, plants in P-limited conditions may inspire many adaptive responses to increase P acquisition by reprogramming metabolism and restructuring root system architecture to maintain a high growth rate (Vance et al. 2003; Jain et al. 2007). For example, plants in P deficient soils have higher root-cap ratios and lower above-ground biomass than the P sufficient soils, in order to reduce nutrient loss, improve nutrient utilization efficiency, and maintain the growth rate. Promoting root growth is another common response of plants to P deficiency. Research has observed the positive root features which include length, surface area, fineness, lateral root formation, root hair density (Wissuwa 2003; Hill et al. 2006; Lynch and Ho 2005; Hermans et al. 2006; Hammond and White 2008), while the root diameter decreases (Wissuwa 2003) in low-P supply soils. P has also been shown by some investigators to be a key element that strongly affects the initiation and growth of cluster roots (Shane and Lambers 2005; Abdolzadeh et al. 2010). By this way, a large root system is formed, which is helpful for P uptake, since the diffusion to the root surface is the rate-limiting step, especially in high P-fixing tropical soils (Gahoonia and Nielsen 2004; Louw-Gaume et al. 2010). Secretion of root exudates (including acid phosphatases, low-molecular-weight organic acid, and proton) is another typical P shortage response of plants (Sas et al. 2001; Vance et al. 2003). George et al. (2006) proved that the increased phosphatase activity in the rhizosphere was related to the depletion of organic P from P-deficient Oxisols, while an increase in organic acid secretion was observed in many species under P deficient conditions

(Carvalhais et al. 2011). As a component of nucleotides which serve as energy storage within cells (ATP) or form the nucleic acids (DNA and RNA), P supply may affect plant genetic properties. The shortage of P may cause a decrease in the quantity of plant seeds, or induce small and low germinating rate of seeds.

Ecologically, P is widely considered to affect the ecosystem primary productivity, species richness and composition, as well as the ecosystem structure and function (Tanner et al. 1998; Seastedt 2001). Crews et al. (1995) indicated that it was the soil P availability that determined the abundance and coverage of the dominant plant species in mountainous rain forests in Hawaii. Turner (2008) found that soil organic P might affect the distribution and co-existence of plant species in lowland tropical forests. In an ombrotrophic peatland in the Republic of Panama, a strong negative relationship between readily-exchangeable phosphate and tree species diversity was observed by Sjögersten et al. (2011). In some European forest ecosystems, P was even more likely to be the cause of species loss than N (Wassen et al. 2005). Moreover, the variation of soil P availability has been found to change epiphyte community structures in some ecosystems (Benner et al. 2007).

Plants also play an important role in P biogeochemical processes. Biogeochemical cycling of P in ecosystems is driven by plant nutrient uptake and maintained by the sustainable supply of soil bioavailable P. Generally, plants absorb phosphates from soils, and then binds them into organic compounds. Different plant species or a plant species in different growth periods have different absorption and utilization capacities. Lodhiyal and Lodhiyal (2003) found that the nutrient uptake was highest in trees, followed by shrubs and herbs; P concentrations were lower in the younger plant parts than in its old counterparts. Due to plant absorption, bioavailable P in soils is fixed by plants, and its concentrations follow the orders in different plant tissues: reproductive parts > leaf > bole bark > branch > bole wood in aboveground part, and fine roots > lateral roots > stump root in belowground part (Lodhiyal and Lodhiyal 2003). In addition, due to plant absorption effect, the P concentration gradient is observed from plant rhizospheres to bulk soils,

which induces soil P transportation from bulk soils to rhizospheres.

Root exudates (including acid phosphatases, low-molecular-weight organic acid, and proton) secreted by plants are also involved in P biogeochemical processes, and are known to play an important role in the mobilization of sparingly soluble nutrients in the rhizosphere (Vance et al. 2003; Wang et al. 2008; Carvalhais et al. 2011). Extracellular acid phosphatases are responsible for the hydrolysis of organic P (Richardson et al. 2005). Organic acid from roots is widely considered to improve P nutrition by mobilizing sparingly-available pools of P into the soil solution (Ström et al. 2005; Long et al. 2008; Richardson et al. 2011); especially, organic acids such as citrate, malate and oxalate are likely to be the most common and effective root exudates in the mobilization of P (Ström et al. 2005). The ions balancing organic acid anions released from root cells can change the effectiveness of the ligand exchange reactions (Richardson et al. 2011). The carbohydrate exudates released by plants may also indirectly change soil P forms by stimulating germination and the growth of mycorrhizal fungi, which are known to improve the P availability (Schwab et al. 1991).

In addition to the P uptake from soils, plants also return P to soils by plant litter, root decay, root exudates, trunk runoff and so on, constituting P cycling in the plant-soil system. Researchers have indicated that plant-returned P was the main source of soil bioavailable P in many ecosystems. Lodhiyal and Lodhiyal (2003) found that P returned by litter in the forest of central Himalaya was 5-7 kg P ha⁻¹ yr⁻¹. Although it is still not clear about the amount of P returned by root release as rhizodeposits, it should be large considering the large amounts of C-containing compounds released from roots (Dakora and Phillips 2002), which is estimated to represent approximately 11% of net fixed C and 27% of C allocated to roots (Jones et al. 2009).

There is a close interaction between plants and soils, which ensure the high use efficiency and low loss of P from ecosystems. Until now, the P demands of plants, critical threshold for plant P limitation, composition of P forms in soils, as well as bioavailability of soil P have still been important

issues in the P biogeochemical cycle in the terrestrial ecosystem.

5 Modeling P Biogeochemical Cycles

Using models to simulate nutrient biogeochemical cycles is an effective approach, since field observation and monitoring are often difficult and inaccurate. However, models are rarely used to describe the terrestrial P biogeochemical cycle. Buendia et al. (2010) proposed a semi-mechanism model simulating the P biogeochemical cycle. This model describes each P biogeochemical process in soils using several empiric equations, and presents the dynamics of five P pools using several ordinary differential equations. The model can not only estimate different P pools in a steady state in which uplift equals erosion, but also calculate the dynamics of different P pools in a watershed where a steady state does not reach (for example, in a constant uplift), and predict when a steady state can be reached (Buendia et al. 2010). Meanwhile, the model can clarify how tectonic uplift, climate, vegetation, and exogenous inputs interact to maintain the active P-cycle in the terrestrial ecosystem under different hydroclimatic conditions. It emphasizes the important influence from tectonic uplift on P inputs. By using the model in Franz Josef and Hawaiian Chronosequences, the tectonic uplift is a fundamental constraint on P delimitation in humid ecosystems, and the hydroclimatic conditions control the P loss and accelerate the formation of the steady state. Additionally, the model may be integrated into global climate models to provide P pools as input data, since it can be implemented with a limited number of parameters.

6 Conclusions and Perspectives

Mountain ecosystem provides an ideal area to integrate geochemical, hydrological, biological and ecological processes for comprehensively understanding the biogeochemical cycling of P. Moreover, research on P biogeochemistry in the mountain ecosystem is an important aspect of biogeochemistry, ecology, biology, environmental sciences and global changes. The mountain

ecosystem, sensitive to global change, is a unique terrestrial unit and plays a vital role in environmental change in lowland aquatic systems. Its development is limited by the P bioavailability. However, former research on the biogeochemical cycling of P was mainly carried out in the forest, grassland, agriculture land, aquatic region and even in the laboratory. A lot of research has been performed focusing on weathering and P release, P fraction transformation and bioavailability, interaction between the P biogeochemical cycle and microbes and plants, as well as model development for accurate simulation of the P biogeochemical cycle. Particular research in mountain ecosystem has seldom been reported.

Most of earlier research was aimed at specific processes in the P biogeochemical cycle, such as weathering, microbial and plant functions and feedbacks. However, there still exist some arguments even over the basic approaches. For example, how can we accurately estimate P release by rock weathering? The weathering rate of apatite is quite different from that of silicate minerals, and thus it would be misleading to use the P/Si ratio to assess the P release rate. It is necessary to integrate all aspects and researches on soils, microbes,

plants and even water bodies to obtain a comprehensive understanding of the P biogeochemical cycle in the mountain ecosystem. A practical biogeochemical model needs to be developed to predict the impact of P biogeochemical cycle on ecological evolution in mountain regions and on the environmental changes in lowland aquatic systems. The model should concern more aspects about the P biogeochemical cycle and combine with other distributed models, such as the distributed hydrological model to improve its accuracy and reliability in modeling P biogeochemical processes.

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