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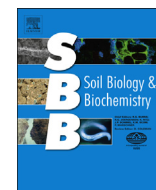

Mineralogical impact on long-term patterns of soil nitrogen and phosphorus enzyme activities

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ABSTRACT

During long-term ecosystem development, both soil mineralogical composition and nutrient contents change, thus possibly altering microbial nutrient cycling by constraining substrate accessibility. In addressing the mineral impact on nitrogen (N) and phosphorus (P) cycling, we determined microbial abundances, activities of N-hydrolyzing (aminopeptidases, protease, urease) and P-hydrolyzing (phosphatase) enzymes and the potential substrate availability as well as their physicochemical and mineralogical controls in whole soil profiles along the 120 kyr-old Franz Josef chronosequence (New Zealand). Pedogenic soil iron (Fe) and aluminum (Al) resided initially (<1 kyrs) in metal-humus complexes, changed to poorly crystalline Fe and Al at intermediate-aged sites (1–12 kyrs) and into dominance of clay and crystalline Fe oxides at the oldest site. Despite this, organic C (OC) and organic N (ON) stocks increased only slightly with soil age, whereas organic P (OP) stocks decreased continuously. In organic layers, enzyme activities were mainly regulated by ON and OP concentrations, whereas in mineral soils, mineral–enzyme relations were more complex and included both, direct and indirect effects. Protease, urease, and phosphatase activities were inhibited by mineral interactions, especially with poorly crystalline Fe and Al oxides, whereas aminopeptidases were less affected by mineralogical properties On a pedon basis, most N-hydrolyzing enzyme activities per ON stocks responded negatively to increasing stocks of poorly crystalline Fe and Al minerals, but were also affected by the C:N ratio of labile organic substrates. Profile-based phosphatase activities per OP stock were highest at the oldest sites having the largest stocks of clay and crystalline Fe oxides. Overall, our study indicates that long-term mineral changes create distinct patterns of nutrient accumulation and N- and P-enzyme activities at both horizon and pedon scale, with a variable extent of the mineralogical effect for the different N-hydrolyzing enzymes.

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1. Introduction

Extracellular enzyme activities drive many soil ecosystem functions and also provide a useful tool to monitor microbial activity. Soil microorganisms excrete extracellular enzymes to degrade complex organic compounds into small utilizable molecules for microbial assimilation. This process is considered to be the rate limiting step in the decomposition of organic matter (OM) and nutrient mineralization (Sinsabaugh, 1994). The enzyme production is regulated by the environmental nutrient status because it is both energy intensive and requires nitrogen (N) and therefore indicates microbial nutrient demand (Sinsabaugh et al., 2008). This is reflected by the negative relationship between extracellular enzyme activity and the availability of assimilable nutrients (Olander and Vitousek, 2000; Allison and Vitousek, 2005; Allison et al., 2007). Therefore, enzyme activities depend on enzyme stability itself and the accessibility and quality of potential substrates.

What remains poorly understood is how enzyme activities are altered by abiotic factors such as the mineralogical soil composition

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(Allison, 2006; Marinari and Vittori Antisari, 2010; Achat et al., 2012). Variation in soil mineral assemblage can cause a differential accumulation and stabilization of organic forms of carbon (OC), nitrogen (ON), and phosphorus (OP) (Mikutta et al., 2009, 2010; Vincent et al., 2012). Soil enzyme activities can also be affected directly by mineralogical composition. For example, enzymes can be stabilized against degradation and proteolysis by clay minerals, whereas their activities can be inhibited due to sorption onto the surface of clay minerals (Nannipieri and Smalla, 2006) or enhanced by the presence of allophane (Allison, 2006). Besides direct effects, minerals can exert several indirect effects on enzyme activity. Organic substrates can be adsorbed onto mineral surfaces (Kalbitz et al., 2005; Mikutta et al., 2007) or complexed and precipitated with iron (Fe) or aluminum (Al) (Nierop et al., 2002; Scheel et al., 2007), thus, resulting in a reduced bioavailability (Allison and Jastrow, 2006). Organic matter strongly bound to minerals is typically less accessible to microorganisms (Kaiser et al., 2007), whereas the presence of an easily desorbable OM pool promotes microbial activity (Mikutta et al., 2007). These strong organo-mineral interactions, particular in subsoil horizons, can deplete concentrations of dissolved nutrients (ON, OP) in the soil solution, potentially causing an up-regulation of enzyme activities. The mineralogical composition of soil, however, changes with ongoing weathering and soil formation and results in varying interaction processes with soil OM (Torn et al., 1997; Mikutta et al., 2009, 2010). Most studies of enzyme activities have focused on topsoil horizons (Allison et al., 2007; Baldrian et al., 2008), and little is known about the dynamics of ON and OP in relation to microbial activity on a pedon scale, even though a large fraction of soil OM is contained in mineral subsoil horizons (Kaiser and Guggenberger, 2000; Moore and Turunen, 2004).

Here, we test whether the activities of N- and P-hydrolyzing enzymes depend solely on N and P abundances, or are altered throughout soil development because of shifts in mineral assemblage from primary silicates to more protective minerals like poorly crystalline and crystalline Fe and Al phases (Torn et al., 1997; Mikutta et al., 2009). We used a chronosequence to test these ideas because it is a powerful space-for-time approach for assessing changes in soil properties and processes (Stevens and Walker, 1970; Wardle et al., 2004). During long-term soil development nutrient concentrations change. Nitrogen limits during primary succession and accumulates over time due to atmospheric inputs and biological N_2-fixation while phosphorus (P) is initially high and becomes increasingly scarce as a result of weathering of P-containing minerals and leaching (Walker and Syers, 1976; Crews et al., 1995; Peltzer et al., 2010). We hypothesize that changing mineralogical properties with soil age, directly and indirectly control microbial N and P enzyme activities. Specifically, we focus on enzyme regulation mechanisms in whole soil pedons, including organic and mineral horizons, in relation to nutrient concentrations and their potential accessibilities. For that, we determined microbial abundances and activities of N- and P-hydrolyzing enzymes and investigated their controls based on soil physicochemical and mineralogical properties along the 120 kyr-old Franz Josef soil chronosequence in New Zealand (Stevens, 1968; Almond et al., 2001). Storage of OC, ON, and OP along the sequence were analyzed and the potential substrate availability of OM was tested in desorption experiments.

2. Material and methods

2.1. Sites and soil sampling

The Franz Josef chronosequence is located on the West Coast on the South Island of New Zealand (~43° S, 170° E). The soils developed due to repeated glacial advance and retreat from greywacke and mica schist spanning a time scale from present to 120 kyrs. The two oldest sites also received loess depositions (Stevens, 1968; Almond et al., 2001). The mean annual temperature is 10.8 °C; precipitation at the youngest four sites is ca. 6500 mm and ca. 3500 mm at the three older sites. Soils are covered by temperate rainforest with a general dominance of evergreen angiosperms. Woody plant diversity, vegetation cover and tree height increase through ecosystem progression, and then decline (Richardson et al., 2004).

Soil samples from seven sites were collected in January 2012. From three randomly chosen profiles per site, every genetic horizon was sampled to a soil depth of 1 m, thus, three site replicates were available for laboratory analyses. For determination of soil bulk density and soil moisture, samples were taken with 100 cm^3 cylinders. For total cell counts, a 1-mL fresh soil mini-core taken by a truncated syringe was fixed with 2% (vol./vol.) formaldehyde in 0.9% NaCl solution and shaken vigorously. All soil samples for microbial analysis were kept at <4 °C prior to analysis.

2.2. Soil parameters

Moist soil material was sieved through a 2-mm sieve and subsequently air-dried. Samples taken with 100 cm^3 cylinders were dried at 60 °C to a constant weight to calculate bulk density and soil moisture. Soil pH was measured in distilled water (1:2.5; wt./vol.). Total C (TC) and total N (TN) contents were measured by a CNS analyzer (Vario EL III; Elementar Analysensysteme GmbH, Hanau, Germany). Soil samples did not contain carbonate due to the acidic conditions, therefore TC was equivalent to OC. Inorganic N ($[Nmin] = [NO_3^-] + [NH_4^+]$) was extracted from field moist samples with 1 M KCl (1:10 wt./vol.), kept frozen until analysis and was determined photometrically (SAN-plus, Skalar Analytical B.V., Breda, The Netherlands). Organic N was calculated as the difference between TN and Nmin. Total P (TP) and OP contents of soils were analyzed using the ignition method of Saunders and Williams (1955) with photometric detection of the blue P-molybdate complex at 880 nm (Schinner et al., 1993). Selective extractions of oxalic oxalate-extractable Fe and Al (Fe_o, Al_o) and dithionite–citrate–bicarbonate-extractable Fe (Fe_d) were performed on bulk soil samples according to Schlichting et al. (1995). Acid oxalate dissolves Fe and Al from poorly crystalline minerals and metal–humus-complexes while dithionite–citrate–bicarbonate extracts pedogenically formed Fe phases including poorly crystalline and crystalline Fe oxides as well as Fe–humus complexes. The difference between dithionite–citrate–bicarbonate extractable Fe and oxalic oxalate-extractable Fe represents crystalline Fe phases (Fe_{d-o}). Extraction of Fe and Al from organic complexes (Fe_p, Al_p) was accomplished with 0.1 M sodium pyrophosphate ($Na_4P_2O_7$, pH 9.5) at a solid-to-solution ratio of 1:50. Solutions were flocculated with 5 mL of 0.05 M $MgSO_4$ and 5-mL aliquots were centrifuged at 300,000 *g* for 6 h. Fe and Al concentrations in extraction solutions were measured by inductively coupled plasma atomic-emission spectroscopy (Varian 725-ES, Varian Inc., Palo Alto, California, United States). Particle size distribution of horizons was determined after removal of Fe oxides and OM by standard pipette analysis (Schlichting et al., 1995).

2.3. Potential substrate availability

In order to test the potential availability of OM for enzymatic reactions, two desorption experiments were conducted. First, field moist soil samples were extracted with 0.5 M K_2SO_4 (1:4 wt./vol.) for OC and TN. The K_2SO_4-extractable fraction was considered to be a highly bioavailable OM pool (Balser and Firestone, 2005). Second, dry soil samples were extracted with 0.1 M NaH_2PO_4 (1:25 wt./vol.) for 17 h, centrifuged (30 min, 3500 *g*) and filtered (0.45 μm,

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