



Soil enzyme activity and stoichiometry in forest ecosystems along the North-South Transect in eastern China (NSTEC)



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ABSTRACT

Soil enzymes, as indicators of microbial metabolism, play an important role in nutrient biogeochemistry at the ecosystem level. In this study, we present information from a comprehensive analysis of the latitudinal variations in, and stoichiometric relationships between, soil β -glucosidase (BG), *N*-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP), and acid phosphatase (AP) in nine forest ecosystems along the North-South Transect in eastern China. The results showed that soil BG and NAG activities were higher in temperate forests than in subtropical and tropical forests. Soil AP activities were the opposite, which indicates that microbial nutrient demand in tropical forests was limited by the nutrient phosphorus (P). Soil BG and NAG activities were significantly and negatively correlated with mean annual temperature (MAT), mean annual precipitation (MAP), the soil carbon (C):P and soil nitrogen (N):P ratios, but not with the soil C:N ratio. Soil NAG and AP activities were inversely correlated with soil pH, and soil AP activity increased as soil pH decreased. The latitudinal variations in the C:N, C:P, and N:P acquisition ratios represented by $\ln(\text{BG}):\ln(\text{LAP} + \text{NAG}):\ln(\text{AP})$ activities across ecosystems were significantly and negatively related to MAP and MAT. The C:P and N:P acquisition ratios were positively related to soil pH but negatively related to the soil C:P and N:P ratios. The C:N and C:P acquisition ratios were also negatively correlated with leaf C:N, C:P, and N:P ratios. This study provides useful information about environmental controls on enzyme stoichiometry, and also highlights the stoichiometric and energy limitations on the metabolism of soil microbes.

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1. Introduction

Forest vegetation and soils contain about 1240 Pg of carbon (C), of which about two-thirds of this amount is accounted for by soils (Dixon et al., 1994), representing a considerable contribution to the

global C cycle. It is also thought that forest soils have a high potential to sequester atmospheric carbon dioxide (IPCC, 2000; Lorenz and Lal, 2010). Variation in this C store could influence global C and nutrient cycles, global climate change, and vegetation patterns. The ecosystem C storage ability may be limited by the balance of multiple elements and the supplies of nitrogen (N) or phosphorus (P) (Hessen et al., 2004). Soil enzymes, as indicators of microbial nutrient demand and metabolism processes, play an important role in soil organic carbon mineralization (Burns and Dick, 2001). Therefore, studies of the stoichiometry of the soil enzymes responsible for C, N, and P mineralization will provide insights into the influence of microbial mechanisms on regional C cycling. Further, studies of ecosystem nutrient acquisition ratios are

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urgently needed because of their association with the threshold at which control of community metabolism shifts from nutrient to energy flow (Sinsabaugh et al., 2009).

The stoichiometry theory is used to calculate the relative quantities of reactants and products in chemical reactions; and ecological stoichiometry involves studying the regulation of living organisms as they assimilate resources from exterior environments (usually C, N, oxygen (O), P, and sulfur (S)) (Sterner and Elser, 2002). Stoichiometry has been extended to study the relative quantities of elements and ecosystem function (Ågren, 2004; Cleveland and Liptzin, 2007; Sinsabaugh et al., 2008, 2009). An increasing number of studies have identified the consequences of systematic variations in the C:N:P stoichiometry of organisms (Sterner and Elser, 2002; McGroddy et al., 2004; Cleveland and Liptzin, 2007). For example, the mean C:N:P ratios of plant foliage and litter were approximately 1212:28:1 and 3000:46:1, respectively (McGroddy et al., 2004; Reich and Oleksyn, 2004). Microbial respiration and nutrient immobilization increase the N and P content of litter as it decomposes, eventually resulting in higher amounts of N and P in soil organic matter (186:13:1) and even higher concentrations of N and P in microbial biomass with a mean C:N:P ratio of 60:7:1 (Cleveland and Liptzin, 2007). Studies have reported C:N:P stoichiometry of 287:17:1 and 42:6:1 for soil nutrient and soil microbial biomass, respectively, at the global scale, but there is wide variation between biomes (Xu et al., 2013). Researchers have also suggested that the activities of hydrolytic enzymes can act as indicators of microbial nutrient demand, and that there are also stoichiometric relationships between the enzyme activities of the different functions responsible for C, N, and P mineralization (Sinsabaugh et al., 2008, 2009).

Many studies of soil extracellular enzyme activity (EEA) (Burke et al., 2011; Lucas-Borja et al., 2011; Brzostek et al., 2012; Marklein and Houlton, 2012) have also examined the ecological stoichiometry of soil EEA. Because EEA links environmental nutrient availability with microbial production, large-scale patterns in EEA may provide information on the constraints of microbial biomass stoichiometry and enzyme relationships on SOM composition. The most-frequently measured activities include β -1, 4-glucosidase (BG, which catalyzes the terminal reaction in cellulose degradation), β -1,4-N-acetylglucosaminidase (NAG, which catalyzes the terminal reaction in chitin degradation), leucine aminopeptidase (LAP, which hydrolyzes leucine and other hydrophobic amino acids from the N-terminus of polypeptides), and acid or alkaline phosphatase (AP, hydrolyze phosphate esters including phosphomonoesters, phosphodiester, and in some cases phosphosaccharides that release phosphate) that are frequently linked to rates of microbial metabolism and biogeochemical processes (Schimel and Weintraub, 2003; Moorhead and Sinsabaugh, 2006). Ratios of common components of soil EEA, such as BG, NAG, LAP, and AP, can be used as indicators of the allocation of C, N, and P. A global-scale meta-analysis based on data from 40 ecosystems showed that the ratios of soil specific C, N, and P acquisition efforts of hydrolytic enzyme activities are close to 1:1:1 (Sinsabaugh et al., 2008). These analyses were extended and the authors found that there were similar stoichiometry ratios in the enzyme activities of C, N, and P in terrestrial soils and fresh water sediments (Sinsabaugh et al., 2009). This means that the supply rates of assimilable substrates from the respective C, N and P reservoirs are generally similar in magnitude.

The C:N:P ratio of enzyme activities may be influenced by climate, vegetation, soil properties, and human activities. Sinsabaugh et al. (2008) found that all activities were significantly related to soil pH. However, the BG:AP activity ratio was inversely related to the mean annual temperature (MAT) and precipitation (MAP), while the ratio of BG:(NAG + LAP) activities increased with MAP. In tropical forests, the BG:AP and NAG:AP ratios were

significantly lower than those of temperate ecosystems and were also regulated by MAT and MAP (Waring et al., 2014). The cycling of nutrients between soils and plants is mediated by microbes and the enzymes that they produce to depolymerize organic substrates. There is therefore a strong theoretical basis for predicting that the stoichiometries of plants, microbes, enzymes and soil are coupled (Sterner and Elser, 2002). Previous studies have been mainly at the global (Sinsabaugh et al., 2008), catchment (Hill et al., 2012) and plant species levels (Bell et al., 2014), and the relationship between the stoichiometry of soil enzymes and climate and soil pH has also been examined. Although soil EEA stoichiometry has been studied, it remains important to develop a better understanding of how climate, substrate availability, and nutrient ratios influence enzymatic stoichiometry of soil.

The ecological stoichiometric ratios of ecosystem components (plants, litter, and soil) can highlight factors that limit biogeochemical cycling (Gundersen et al., 1998; Ollinger et al., 2002; Güsewell et al., 2003; Tessier and Raynal, 2003), and have been used increasingly to predict ecosystem productivity and C cycling (Sterner and Elser, 2002). For example, the soil C:N ratio is significantly correlated with chemical nutrients in the canopy, the C:N ratio of litter, and nitrification and denitrification of soil N (Gundersen et al., 1998; Ollinger et al., 2002). Soil biomass C:P and N:P ratios can be used as indicators of N and P availability to microbes, and may indicate the degree of deficiency in the N or P supplied to plants (Güsewell et al., 2003; Tessier and Raynal, 2003). When the soil C:P ratio is larger than 186, the ecosystem nutrient cycles are P-limited (Sinsabaugh et al., 2009). Foliage N:P ratios have also been used to assess nutrient limitation and indicate N saturation (Tessier and Raynal, 2003). Extracellular enzymes synthesized by soil microbes are the rate-limiting step for microbial metabolism (Jones et al., 2009). The ecoenzyme stoichiometric ratios reflect the ability of microorganisms to use nutrients (Schimel and Weintraub, 2003; Moorhead and Sinsabaugh, 2006; Jones et al., 2009). For example, the BG:AP activity ratio indicated that nutrient cycling in tropical forests ecosystems was P-limited (Waring et al., 2014). It was also found that P availability could influence C cycling in the highly weathered, P-limited soils. Ratios of common measures of soil EEA, such as BG, NAG, LAP, and AP, can be used as indicators of the allocation of microbial resources to acquire C, N, and P (Waring et al., 2014). Eco-enzyme stoichiometric ratios can also provide a biological perspective on the influence of catchment scale and anthropogenic disturbances on the nutrient balance (Hill et al., 2012). For example, based on the water chemistry and sediment enzyme activities, many biofilms were P-limited and sediments were C- and N-limited (Hill et al., 2012). The stoichiometry of ecoenzymatic activity can also be used in biogeochemical equilibrium models to study the relationship between the microbial nutrient demand and nutrient availability. It also indicates switches in ecological system metabolism from energy flows, represented by C, to flows of limiting nutrients, represented by P or N (Sinsabaugh et al., 2009).

The North-South Transect of Eastern China (NSTEC) represents a latitudinal and temperature gradient and is one of fifteen international standard transects established as part of the Global Change and Terrestrial Ecosystems initiative (Canadell et al., 2002), and a key component of the International Geosphere-Biosphere Programme (IGBP) (Peng and Liu, 2002). It is a unique belt in which vegetation ranges from boreal forest to tropical rain forest, depending on the local temperature and precipitation conditions. From North to South, mean annual temperatures (MAT) vary from -7°C in the cold, temperate, continental monsoon climatic zone to over 26°C in the equatorial monsoon climatic zone; mean annual precipitation increases from less than 500 mm in the cold temperate zone to about 2266 mm in the tropical rain forest zone.

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