



## Review

## Microbial extracellular enzymes in biogeochemical cycling of ecosystems

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## ABSTRACT

Extracellular enzymes, primarily produced by microorganisms, affect ecosystem processes because of their essential roles in degradation, transformation and mineralization of organic matter. Extracellular enzymes involved in the cycling of carbon (C), nitrogen (N) and phosphorus (P) have been widely investigated in many different ecosystems, and several enzymes have been recognized as key components in regulating C storage and nutrient cycling. In this review, it was the first time to summarize the specific extracellular enzymes related to C storage and nutrient cycling for better understanding the important role of microbial extracellular enzymes in biogeochemical cycling of ecosystems. Subsequently, ecoenzymatic stoichiometry - the relative ratio of extracellular enzyme, has been reviewed and further provided a new perspective for understanding biogeochemical cycling of ecosystems. Finally, the new insights of using microbial extracellular enzyme in indicating biogeochemical cycling and then protecting ecosystems have been suggested.

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## 1. Introduction

Extracellular enzymes, ubiquitous in soils/sediments, play essential roles in decomposition of soil/sediment organic matters (SOM) so as to meet the nutrient and energy demands of microbial growth (Allison and Vitousek, 2005; Moorhead et al., 2012; Sinsabaugh, 2010). Microbial decomposers, mostly being bacteria and fungi, synthesize and excrete extracellular enzymes to obtain assimilable organic monomers or mineral nutrients for their uptake (Allison et al., 2011; Mooshammer et al., 2014). The available substrates are basis for building up microbial biomass and synthesizing extracellular enzymes (Mooshammer et al., 2014). According to economic principle, microorganisms would not synthesize or secrete extracellular enzymes when available energy and nutrients are enough for their growth (Allison et al., 2011; Dick, 2011). From this aspect, it can be deduced that the production of microbial extracellular enzymes (MEEs) should be closely related to the availability of environmental resources. Therefore, MEEs may be used as good indicators for nutrient cycling in different ecosystems. However, once extracellular enzymes released into the environment, the decomposers or hosts have little control over their functions and fates (Allison et al., 2007; Burns et al., 2013). Different from gene expression, the activities of MEEs are not only affected by the changes of environmental factors (e.g., temperature, pH, heavy metals, etc.), but also by the physical structure and texture of soils/sediments (Allison et al., 2007; Freeman et al., 2004; Sinsabaugh, 2010; Van Bodegom et al., 2005). Thus, MEEs may also indicate soil quality as well as the environmental contaminations (Crowther et al., 2011; Knight and Dick, 2004).

During the past 100 years, most research on MEEs has focused on the kinetics and spatiotemporal variations of MEEs activities in different ecosystems, such as wetlands, forests, deserts, and so on (Moscatelli et al., 2012; Sistla and Schimel, 2013; Wallenstein et al., 2011). On a global scale, Sinsabaugh et al. (2008) found the activities of hydrolases were more closely related to SOM content, while the activities of oxidases were more affected by soil pH. This finding suggested that hydrolases might be more important for SOM decomposition, and thus affecting nutrient and C cycling. However, Freeman et al. (2001) proposed an 'enzymic latch' on global C store, which emphasized the key role of phenol oxidase in regulating hydrolase and then SOM decomposition. In recent years, a new term - coenzymatic stoichiometry (ES) has been emerged to indicate the microbial nutrient limitation of soils/sediments, and may predict SOM decomposition and C cycling to some extent. Briefly, ES links extracellular enzymes activities to microbial resource allocation under different environmental conditions (Luo et al., 2017; Sinsabaugh and Follstad Shah, 2012; Waring et al., 2014). From this perspective, ES may be used as good indicator for microbial nutrient acquisition and then reflect SOM decomposition under environmental changes. Based on the above-mentioned studies, it is well known that hydrolases, phenol oxidase, and ES are of importance in ecosystem processes such as SOM decomposition and C cycling, however, there is still uncertainty about their role in biogeochemical cycling of ecosystems and also there is no relevant review to summarize these information together.

Considering the crucial role of MEEs in ecosystem processes, this review systematically summarized the relevant information about

MEEs in biogeochemical cycling of ecosystems. At the beginning, it briefly introduced the origins, locations, distributions and assay methods of MEEs activities. Subsequently, it was the first time to review the current knowledge about several key MEEs involved in C, N and P cycling as well as the influence of nutrient inputs on these MEEs in ecosystems. Thereafter, the implication of enzymatic stoichiometry in biogeochemical cycling of ecosystems was further discussed. At the end of this review, several suggestions were proposed for the future studies.

## 2. Origins, locations and distributions of MEEs

### 2.1. Origins

Nowadays, it is clear to us that microorganisms are the major sources of MEEs in soils/sediments, but an erroneous conclusions were proposed in earlier research. As early as 1899, plant roots were found to be able to produce peroxidases, and then found to secrete amylase, invertase, catalase, tyrosinase, etc., causing a misunderstanding that the major sources of extracellular enzymes were plants originated (Dick, 2011). Along with the development of technologies, microorganisms have been gradually revealed and considered as the critical sources of soil enzymes (Arnosti, 2011; Sistla and Schimel, 2013). Moreover, some other organisms such as insects, invertebrates, fauna, and so on may also partially contribute to the soil enzyme pools (Gianfreda and Rao, 2014).

In recent decade, the evolution of molecular techniques has enabled investigation on the correlation between gene expression and enzyme activity, offering a better way to understand the origins of MEEs as well as yield insights into the complex physiological responses of microorganisms to environmental changes (Arnosti, 2011). For example, the fungal and bacterial genes of laccases have been explored in forest soils, and their crucial roles in soil C cycling have been highlighted (Kellner et al., 2008, 2009; Luis et al., 2004). However, the relevant data about the application of molecular technologies in soil enzymes are still less recorded due to the complexity of soils and difficulties to design the PCR primers for targeting enzyme-encoding genes.

### 2.2. Locations and distributions

Generally, there are two kinds of enzymes in soils, i.e., constitutive and inducible enzymes. Constitutive enzymes (e.g., pyrophosphatase) always present in nearly constant amounts, while inducible enzymes (e.g., amidase) are only produced in response to specific substrates (Arnosti, 2011; Das and Varma, 2011). In fact, enzymes are not only secreted by living microorganisms and plant roots actively, but also released by the dead biota after cell lysis (Quiquampoix et al., 2002). Once enzymes released into soils, they are probably adsorbed by surface-reactive particles or entrapped in the mineral and humic substances (Gianfreda and Rao, 2014; Marx et al., 2005; Nannipieri et al., 2012). Therefore, it can be known that free enzymes are normally short-lived. On the other hand, enzymes may be associated with the microbial cell's plasma membrane, contained within soil aqueous phase and attached onto the mineral and organic matter as well as mineral-organic aggregates (Burns et al., 2013; Wallenstein and Burns, 2011). Although MEEs activities bound to cells and immobilized onto soil colloids may be

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