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Enzyme activities as a component of soil biodiversity: A review

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Summary

Soil enzyme activities are the direct expression of the soil community to metabolic requirements and available nutrients. While the diversity of soil organisms is important, the capacity of soil microbial communities to maintain functional diversity of those critical soil processes through disturbance, stress or succession could ultimately be more important to ecosystem productivity and stability than taxonomic diversity. This review examines selected papers containing soil enzyme data that could be used to distinguish enzyme sources and substrate specificity, at scales within and between major nutrient cycles. Developing approaches to assess soil enzyme functional diversity will increase our understanding of the linkages between resource availability, microbial community structure and function, and ecosystem processes.

Introduction

Understanding and maintaining biodiversity has become an increasingly important field of research, as well as a resource management goal. In soil microbial communities, maintaining critical functions may ultimately be more important than maintaining taxonomic diversity. One essential microbial function in soils is the processing and recovery of key nutrients from detrital inputs and accumulated soil organic matter. This often requires the activity of extracellular enzymes to process complex organic compounds into assimilable subunits (sugars, amino acids, NH_4^+, PO_4^{-3}). The field of soil enzymology, including numerous methods and applications, has been extensively reviewed (Burns, 1978; Burns and Dick, 2002).

Soil enzyme activities have been related to soil physio-chemical characters (Amador et al., 1997), microbial community structure (Waldrop et al., 2000; Kourtev et al., 2002), vegetation (Waldrop et al., 2000; Sinsabaugh et al., 2002), disturbance (Bolton et al., 1993; Eivazi and Bayan, 1996; Garcia and Hernandez, 1997; Boerner et al., 2000), and succession (Tscherko et al., 2003). Scales of resolution have ranged from the landscape (Bonmati et al., 1991; Decker et al., 1999; Amador et al., 1997) to soil particle size fractions

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(Kandeler et al., 1999). Equations to assess soil quality have included various enzyme activities (Halvorson et al., 1996; Pankhurst et al., 1997; Trasar-Cepeda et al., 1998; Saviozzi et al., 2001; Killham and Staddon, 2002; Speir and Ross, 2002). Soil enzyme data have been the foundation for the development of conceptual models that provide a more comprehensive understanding of those key processes linking microbial populations and nutrient dynamics (Sinsabaugh and Moorhead, 1994; Schimel and Weintraub, 2003). While these studies have typically dealt with differences in soil enzyme activities, it is also possible with these assays to develop specific measures of functional diversity.

Distinct from the physiological or genetic diversity of the soil microbial biomass (Zak et al., 1994; Kennedy and Grewin, 1997; Emmerling et al., 2002; Wellington et al., 2003) which assess *potential*, functional diversity of soil enzymes is related to the actual *activities* resulting from that potential. Functional enzyme diversity can be determined from several interacting sets of information, either independently or interactively. These include the measurements of activities against target substrates from the major nutrient resources, distinguishing different reaction mechanisms to activities within a given enzyme function (e.g., proteolysis), and the possible determination of enzyme sources. The objectives of this paper are to briefly review previous applications of soil enzyme activities and suggest possible approaches that could be used to assess soil enzyme functional diversity between and within major nutrient cycles.

Substrate specificity

Substrate specificity, as either an independent measure of enzyme diversity or as means to distinguish different reaction mechanisms, could resolve those enzyme activities that attack specific detrital components either between or within major nutrient pools (Table 1). Within each type of nutrient, there are specific chemical forms based on structure and bonding. The major forms of carbon are polysaccharide, aromatic (lignin) and aliphatic (polymethylene). The bulk of organic nitrogen is thought to be the in amide form (Knicker et al., 1997), either as peptide or non-peptide C–N bonds. Most organic phosphorus occurs in either a mono- or di-ester form (Dalal, 1977).

Within each of these major nutrient groups, there are specific compounds against which major classes of soil enzymes are active. Keystone to the breakdown of litter are the various cellulolytic activities requiring endo-cellulases, cellobiohydrolases and β-glucosidases (Sinsabaugh et al., 1992), and ligninolytic activities requiring a variety of polyphenol oxidases and peroxidases (Kirk and Ferrell, 1987). Within the nitrogen cycle, substrate diversity for proteins and peptides can be based on hydrolysis of different amino acid groups (Ladd and Butler, 1972; Tabatabai et al., 2002). Release of ammonium from various non-peptide C–N bonds can also be measured for a variety of different substrates, including the frequently measured urease activity. Mineralization of phosphate from organic esters can be resolved into phosphodiesterase and phosphomonoesterase activities, reflecting the use of tissue-based and soil organic phosphates pools, respectively (Dalal, 1977).

Reaction mechanisms

Since enzyme activities are catalyzed at specific reactive sites, another component of enzyme functional diversity could be based on using specific inhibitors or substrates.

The most common use of inhibitors has been with proteolytic enzymes where four major groups of proteases can be distinguished (Morihara, 1974). While broad generalizations about enzyme source can be made for aspartic- (fungal), thiol- (general), metallo- (bacterial) and serine- (general) proteases, separating proteolytic activity into these four classes also represents a component of functional diversity in itself. Different reaction mechanisms are also found among peptidases, where removal of terminal amino acids is by the selective enzyme binding to either the free amino- or carboxy- end of the peptide. Soil peptidase activities have been measured using either aminopeptidase (Saiya-Cork et al., 2002; Sinsabaugh et al., 2002) or carboxypeptidase substrates (Ladd and Butler, 1972; Kamimura and Hayano, 2000), but not both together in a single study.

Sources of soil enzyme activities

Knowing the sources of specific soil enzyme activities would greatly enhance our understanding of which group(s) of organisms are directly accessing a given nutrient resource, thus providing greater insight into the pathways by which energy and nutrients flow through the soil food web.

Molecular methods are now at the stage where specific functional genes and their expression by