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총 설

A review of factors that regulate extracellular enzyme activity in wetland soils

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습지 토양 내 체외효소 활성도를 조절하는 인자에 대한 고찰

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ABSTRACT: Wetlands constitute a transitional zone between terrestrial and aquatic ecosystems and have unique characteristics such as frequent inundation, inflow of nutrients from terrestrial ecosystems, presence of plants adapted to grow in water, and soil that is occasionally oxygen deficient due to saturation. These characteristics and the presence of vegetation determine physical and chemical properties that affect decomposition rates of organic matter (OM). Decomposition of OM is associated with activities of various extracellular enzymes (EE) produced by bacteria and fungi. Extracellular enzymes convert macromolecules to simple compounds such as labile organic carbon (C), nitrogen (N), phosphorus (P), and sulfur (S) that can be easily taken up by microbes and plants. Therefore, the enzymatic approach is helpful to understand the decomposition rates of OM and nutrient cycling in wetland soils. This paper reviews the physical and biogeochemical factors that regulate extracellular enzyme activities (EEa) in wetland soils, including those of β-glucosidase, β-N-acetylglucosaminidase, phosphatase, arylsulfatase, and phenol oxidase that decompose organic matter and release C, N, P, and S nutrients for microbial and plant growths. Effects of pH, water table, and particle size of OM on EEa were not significantly different among sites, whereas the influence of temperature on EEa varied depending on microbial acclimation to extreme temperatures. Addition of C, N, or P affected EEa differently depending on the nutrient state, C:N ratio, limiting factors, and types of enzymes of wetland soils. Substrate quality influenced EEa more significantly than did other factors. Also, drainage of wetland and increased temperature due to global climate change can stimulate phenol oxidase activity, and anthropogenic N deposition can enhance the hydrolytic EEa; these effects increase OM decomposition rates and emissions of CO_2 and CH_4 from wetland systems. The researches on the relationship between microbial structures and EE functions, and environmental factors controlling EEa can be helpful to manipulate wetland ecosystems for treating pollutants and to monitor wetland ecosystem services.

Key words: biogeochemistry, organic matter decomposition, wetland ecosystem

Wetlands cover ~6% of the land surface and are among the most productive ecosystems in the world (Mitsch and Gosselink, 1993). Wetland soils have unique characteristics such as restricted oxygen supply, accumulation of reduced compounds and humic substances, the presence of an interface between oxidized soil and floodwater, and exchange of dissolved inorganic nutrients between soil and floodwater (Reddy and DeLaune, 2007). Especially, anaerobic conditions restrict the supply of oxygen to microbes, thereby reducing the rate of organic matter (OM) decomposition relative to aerobic conditions and favoring accumulation of recalcitrant OM. As a result, wetlands contain 14% of the world's terrestrial carbon because of high productivity and low OM degradation rates (Schlesinger, 1977). However, human activities such as draining wetland and supplying nutrients to them have affected vegetation types and microbial communities in wetland ecosystems (Zedler and

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Kercher, 2004; Mentzer *et al*., 2006). In particular, reduced water table and increasing temperature due to global climate change could increase decomposition rates of OM, thereby increasing emission of CO_2 and CH_4 from wetland soils (Freeman *et al*., 2001). Thus, understanding of OM decomposition in wetland soils is important for predicting the influence of global climate change on OM degradation rates, as well as on regional nutrient cycling in wetland ecosystems.

Decomposition of OM is the conversion of complex organic molecules to simple organic or inorganic constituents. Various methods can be used to estimate decomposition rates of OM, such as analysis of CO_2 as a byproduct of decomposition, measurement of change in $^{13}C/^{12}C$ ratio, and loss rates of OM (Torn *et al*., 2009). Analysis of EEa is widely used as an index of decomposition rate because of its ease of measurement and inexpensive cost. EEa is well correlated with loss of litter and with the amounts of soil nutrients such C, N, and P (Sinsabaugh and Linkins, 1993).

As the first step in OM degradation, the leached materials of OM are consumed directly by microbes without any further decomposition. The remaining materials are physically fragmented and decomposed by microbial enzymatic hydrolysis and catabolic activities, and fungi and bacteria secret extracellular enzymes that hydrolyze polymers to monomers. Monomers released by extracellular enzymes enter microbial catabolic processes as energy sources or structural components (Weiss *et al*., 1991). Therefore, because most of the OM should be hydrolyzed into monomers by extracellular enzymes before uptake by microbes, the extent of EEa can be a proxy for microbial activity and can represent the ecosystem's capacity to decompose its OM. Also, when nutrient availability is low, microbes increase EEa to increase the supply of inorganic C, N, P, and S (Olander and Vitousek, 2000). Thus, enzyme assays have become useful techniques for monitoring microbial activity and ecosystem stability (Sinsabaughs and Moorhead, 1994).

EEa is affected by physical factors including temperature (Fenner *et al*., 2005a, 2006), pH (Kang and Freeman, 1999; Williams *et al*., 2000), water table (Freeman *et al*., 1996, 1998); chemical factors including addition of C, N, and P, substrate quality (Sinsabaugh and Linkins, 1993; Nannipieri *et al*., 2002); and global climate change (Kang *et al*., 2001, 2005). Therefore, the purposes of this review are to research the effects of physical and chemical properties, and climate change on EEa; and to suggest the limitation and future direction of EEa researches in wetland soils.

Physical Factors Regulating EEa in Wetland Soils

Temperature

Increased temperature can stimulate EEa because microbial activity approximately doubles with a temperature increase of 10°C (Koch *et al*., 2007). Thus, under low-temperature conditions such as tundra or arctic wetland soils, EEa are lower than those of temperate wetland ecosystems, so OM decomposition is retarded in cold site soils. For example, low temperature limited phosphatase activity that had a positive relationship with temperature from 2 to 15°C in fen and swamp wetlands soils (Kang and Freeman, 1999). In addition, increased temperature leads to diffusion of substrates and EE when the soil water starts to thaw in arctic peatlands, wetlands and permafrost soils; this process can accelerate OM decomposition and increase the amount of CO_2 released into the atmosphere (Davidson and Janssens, 2006).

Microbial composition can affect the responds of EEa to increasing temperature. Bacterial enzymes (e.g., cellulase, proteases, and phosphatases involved in mineralization of organic C, N, and P) may show increased EEa as temperature increases, but fungal enzymes (e.g., peroxidase and phenol oxidase involved in degradation of phenolic compounds) may show EEa that does not respond or that decreases as temperature increases because fungi are more adapted to low temperature than are bacteria (Pietlkâinen *et al*., 2005). Thus, the responding of EEa to increasing temperature can be more apparent in the hydrolytic enzymes than lignin decomposing enzymes.

The response of EEa to increasing temperature is also affected by site characteristics such as temperature regime and geographic variation, by acclimation of microbial structure and functions under increasing temperature, and by intrinsic relationships between temperature and substrate quality or nutrient availability (Creeger *et al*., 2014). Thus, the response of EEa to temperature change is very difficult to predict because of the interacting effects of several factors.

Table 1. The factors that regulate extracellular enzyme activities in wetland soils

Categories	Factors	How to influence	Examples	References
Physical factors	Temperature	Increase in microbial growth Increase in substrate diffusion	Positive relations between hydrolytic EEa and temperature	Kang and Freeman (1999), Davidson and Janssen (2006)
		Favor to low temperature	No response or decrease fungal EEa with increase in temperature	Pietlkâinen *et al*. (2005)
	pH	Modification of ionization state of amino acids and enzyme reaction site Influence the interaction between enzymes and humus/clay Increase in microbial diversity	Positive relationship between pH and phosphatase, arylsulfatase, cellulase, protease, and phenol oxidase.	Pulfort and Tabatabai (1988), Freeman *et al*. (1996), Kang and Freeman, (1999), Williams *et al*. (2000), Acosta-Martíez and Tabatabai (2000), Ekenler and Tabatabai (2003), Sinsabaugh (2010)
	Water table	High water table creates anaerobic conditions and reduces ferric oxide to ferrous iron.	Inhibition of ferrous iron to enzymes. Less efficient anaerobic metabolism by water logging.	
		Drought supplies oxygen to microbes producing lignin decomposing enzymes.	Positive relationship between drought frequency and lignin degrading enzymes.	Fenner *et al*. (2005), Fenner and Freeman (2011)
	Particle size of OM	Quality and quantity of organic matter Microbial community composition	EEa of CPOM is higher than that of FPOM. Fungal EEa is higher in CPOM than FPOM.	Sinsabaugh and Findlay (1995), Marx *et al*. (2005), Jakson and Vallarie (2007), Sinsabaugh (2010)
Chemical factors	Carbon	Microbial activity Limiting factor	Increase in hydrolytic EEa with addition of carbon depending on the nutrient states	Martens *et al*. (1992), Sinsabaugh and Moorehead (1994), Shackle *et al*. (2000)
	Nitrogen	Microbial community composition Limiting factor	Shift from fungus-dominated to bacteria- dominated composition by N addition Increase in hydrolytic EEa for short term by N addition Long-term effect of N addition on EEa is various depending on the nutrient state.	Henriksen and Breland, (1999), Frey *et al*. (2004), Bragazza *et al*. (2006), Min *et al*. (2011), Song *et al*. (2014)
	Phosphorous	Limiting factor	Relationship between phosphatase activities and TP contents are different depending on the nutrient state.	Amador *et al*. (1997), Rejamankova and Komarkova (2000, 2005), Wright and Reddy (2001), Chen *et al*. (2003), Penton and Newman (2007)
	Litter chemistry	Litter chemistry affects types of EE and rates of biodegradability Plant species influence litter chemistry	Relationship between litter chemistry and EEa Plant species determine degradation rates and EEa of litter residue.	Aerts (1997), Carreiro *et al*. (2000), Kim (2001), Bertrand *et al*. (2006), Šnajdr *et al*. (2011)
	Root exudation	Induce EE capable of producing limiting nutrients for plants Carbon supply to microbes	Root exudates ammonia production EE under N limited conditions. Root C exudation enhances microbial activity and EEa.	Bowen (1969), Caravaca *et al*. (2005), Kang and Freeman (2007), Huang *et al*. (2012), Korboulewsky *et al*. (2012), Salvato *et al*. (2012), Cui *et al*. (2013)
Climate change	Elevated CO_2	Change in primary productivity, species abundance, community composition and soil respiration	Increases in tannins and lignin contents by increased CO_2 retard EEa. Increases in root exudation enhance EEa.	Cotrufo *et al*. (1994), Cotrufo and Ineson (1995), Eversberger *et al*. (2001), Freeman *et al*. (2004)
	Anthropogenic N deposition	Alleviate nutrient limitation	Increase in hydrolytic EEa	Curtis *et al*. (1994), Gorissen *et al*. (1995), Arnone and Hirschel (1997), Zheng *et al*. (2010)
	Drought	Supply oxygen to microbes	Increase in oxidative EEa	Fenner *et al*. (2005b), Fenner and Freeman (2011)

pH

Change in pH can modify the ionization state of amino acids and enzyme reaction site as well as the interaction between enzymes and humus or clay. Thus, divergence of optimal pH for EEa can inactivate enzymes, resulting in the reduction of OM decomposition rate. Atmospheric acidic deposition such as HSO_3^-, NO_3^-, and SO_4^{2-} led to decrease in pH, and thereby reduced arylsulfatase activity in peat soils, and low pH has been considered as one of the main factors for low decomposition rates in wetland soils (Press *et al*., 1985). However, base cations (e.g., Ca^{2+} and Mg^{2+}) can attach to organic acids and reduce the precipitation and inactivation of enzymes (Wetzel, 1993).

High pH also affects EEa. In bog and fen soils, increase in pH was associated with increase in phosphatase and arylsulfatase activities (Kang and Freeman, 1999). In peatland and marsh soils (Williams *et al*., 2000) and global-scale soils (Singsabaugh, 2010), increase in pH was associated with increased phenol oxidase activity. High pH leads to deprotonate phenols, which reduces the redox potential and increases the solubility of phenols, increasing their potential reaction; it also increases microbial diversity, creating the diversity of the soil enzyme pool (Sinsabaugh, 2010). Lime application to increase soil pH can enhance cellulase and protease (Acosta-Martíez and Tabatabai, 2000; Ekenler and Tabatabai, 2003) activities and can increase microbial biomass in nutrient-limited soils (Aciego Pietri and Brookes, 2008).

Water table

High water table reduces oxygen content, thereby increasing anaerobic metabolism which is less efficient than aerobic metabolism, and resulting in decreased EEa (Schothorst, 1977). Also, anaerobic conditions due to increasing water table stimulate reduction of ferric oxide to ferrous iron that is known to inhibit enzyme activities (Pulford and Tabatabai, 1988; Freeman *et al*., 1990, 1996; Wetzel, 1993). Waterlogging can cause to decrease in phosphatase, arylsulfatase, β-D-glucosidase, and urease activities due to inhibition by ferrous iron (Pulford and Tabatabai, 1988; Freeman *et al*., 1996). A negative relationship between β-D-glucosidase, phosphatase and arylsulfatase activities and the water table has been observed in the northern fen and swamp soils (Freeman *et al*., 1996; Kang and Freeman, 1999) and in tropical peat soils (Kwon *et al*., 2013). Also, β-D-glucosidase and phosphatase activities of upland soils were higher than those of constructed wetlands due to higher oxygen content in upland soils (Kang *et al*., 1998).

Peroxidase and phenol oxidase are involved in the decomposition of the aromatic ring structure in phenolic compounds and these enzymes require oxygen when degrading lignin and humic substances. Thus, a high water table in wetland soils limited phenol oxidase activities, thereby resulting in accumulation of recalcitrant OM in wetland soils (Benner *et al*., 1984; Reddy and DeLaune, 2007). Accumulated phenolic compounds also inhibit other enzyme activities by formation of covalent bonds with proteins (enzyme), thereby retarding OM decomposition in wetland soils (Freeman *et al*., 2001). Phenol oxidase activity was lower in deeper soils than in detritus layers due to decrease in oxygen content with soil depth (Wright and Reddy, 2001), and was negatively correlated with depth of water table in peatland soils (Pind *et al*., 1994). Especially drought induced by global warming in northern peatlands that contain approximately 455 Pg magnitude of organic carbon content could lead to increased oxygen supply in wetland soils; this increase could stimulate phenol oxidase activities and bacterial growth, resulting in increased OM degradation and increased the release of CO_2 to the atmosphere (Fenner *et al*., 2005b; Fenner and Freeman, 2011).

Particle size of OM

Hydrolytic enzyme (cellobiohydrolase, β-D-glucosidase, and β-xylosidase) activities increased with particle size in stream sediments (Sinsabaugh and Findlay, 1995), soils (Marx *et al*., 2005), and swamp soils (Jackson and Vallarie, 2007) because invertebrates and microorganism living on the coarse-particle OM (CPOM) consumed more labile OM, reducing the size of particles and remaining the recalcitrant materials in the fine-particle OM (FPOM). Thus, FPOM had more recalcitrant materials than CPOM. The oxidative enzyme (phenol oxidase and peroxidase) activities also were enhanced with increase in particle size because FPOM can limit the growth of fungal hyphae and increase the importance of attached bacteria (Sinsabaugh and Findlay, 1995; Sinsabaugh, 2010). Newman and Reddy (1992) reported that alkaline phosphatase was

mainly associated with CPOM in lake sediments, indicating that that particulate-bound enzyme complex was more efficient to hydrolyze the OM than the soluble form because it was more stabilized (Rojo *et al*., 1990).

Chemical Factors Regulating EEa in Wetland Soils

Carbon

Organic carbon (C) is comprised of emergent macrophytes, litter, plankton biomass, OM from wastewater loading, and animal and plant remains in wetlands. Organic C is used as an electron donor to provide energy source to microbes, and this reaction drives all biogeochemical processes in wetland soils. Thus, addition of organic C increases microbial biomass and activity, and together these changes increase overall microbial production of extracellular enzymes. Also, addition of C to wetland soil shifts C:N:P ratios of substrates, and can cause N and P to become limiting factors for microbial growth (Shackle *et al*., 2000). As a result, as C content increases, the microbes tend to increase their discharge of phosphatase and chitinase to remediate this limitation.

Addition of organic C greatly increased the hydrolytic enzyme activities (acid phosphatase, alkaline phosphatase, arylsulfatase, chitinase, β-D-glucosidase, dehydrogenase, amidase and urease) during the first few year of experiment, and coincided with an increase in bacterial biomass, but subsequent addition failed to sustain high EEa in the C amended soil (Martens *et al*., 1992). A plausible explanation for the failure to maintain the positive relationship between organic C and EEa is that EEa production is mainly regulated by induction or repression mechanisms, which is determined by nutrient availability in the surrounding systems. For example, if N and P are not limited in the system, microbes suppress N or P-related EE production to save energy (Sinsabaugh and Moorehead, 1994). Therefore, addition of C can increase EEa by stimulating microbial activities, but excessive C can terminate the production of enzymes when adequate nutrients are present in systems.

Nitrogen

Nitrogen is a limiting nutrient in wetland ecosystems, but excessive N inputs can reduce rates of OM decomposition in the long term (Aber *et al*., 1998). N addition causes wetland communities to shift from fungus-dominated to bacteria-dominated composition (Henriksen and Breland, 1999; Frey *et al*., 2004). Because bacteria assimilate C significantly less efficiently than do fungi (Adu and Oades, 1978), the OM decomposition by bacterial communities might be inhibited, resulting in the accumulation of recalcitrant OM such as lignin (Holland and Coleman, 1987). In addition, lignin inhibits other enzyme activities, thereby reducing the rate of OM decomposition. Therefore, N addition can increase decomposition rates of OM by stimulating microbial activities in the short term, but N addition can restrain the degradation of OM in the long term, due to conversion of the microbial community and to inhibition of EEa.

Chronic addition of N significantly increased hydrolytic EEa and microbial biomass under N-limited conditions because N addition alleviated the N demand (Carreiro *et al.*, 2000; Saiya-Cork *et al*., 2002). Thus, in peat bog soils that received their nutrient supply only from atmospheric deposition and were extremely nutrient-limited systems, atmospheric N deposition altered the litter chemistry and promoted enzymatic activity due to removal of N constraints on microbial metabolisms, resulting in enhanced OM decomposition and thereby increasing the amount of CO_2 released to the atmosphere and input of DOC into adjacent to river ecosystems (Bragazza *et al*., 2006). However, under the nutrient saturated conditions, N input did not change or decrease EEa in a constructed wetland and marsh soils because microbes did not spend more energy to activate C, N, S or P acquiring enzymes under nutrient saturated conditions (Min *et al*., 2011; Song *et al*., 2014). Thus, the level of nutrient conditions, such as eutrophic or oligotrophic conditions will determine how the N addition influences EEa in wetland soils.

Phosphorus

Phosphatase activity is important in wetland soils for P regeneration because up to 90% of organic P is in monoester form. Phosphatase activity increased total P (TP) concentrations in P-limited soils (Amador *et al*., 1997; Chen *et al*., 2003), and served as a predictor of OM degradation in wetland ecosystems (Newman and Reddy, 1992; Amador *et al*., 1997; Chen *et al*., 2003). Thus, increasing P content reduced phosphatase activities

in marsh (Rejamankova and Komarkova, 2000, 2005) and the Everglades wetland soils (Wright and Reddy, 2001; Penton and Newman, 2007) because excessive external loading of P alleviated the P limitation, implying that the availability of P in the system was the main factor for regulating phosphatase activity. However, high phosphatase activities were observed under high TP conditions in wetland soils (Wang *et al*., 2010) and in the rhizosediment of salt marshes (Fretias *et al*., 2014). This phenomenon can be explained by that high TC:TP ratio caused by extremely eutrophic condition can stimulate P mineralization, and that P demand for primary production (plant growth) could trigger the production of phosphatase.

Litter chemistry

Decomposition of plant litter is an important process to supply nutrients to wetland ecosystems. Rates of plant litter decomposition in wetland systems are determined by physico-chemical factors (e.g. temperature, pH, exogenous nutrient supply, moisture, oxygen contents, and electron acceptor availability), by microbial population and structure, and by substrate quality such as litter chemistry (Moretto *et al*., 2001; Ross *et al*., 2002; Koukoura *et al*., 2003). As an indicator of litter quality, C:N, C:P, lignin:N, and N:P ratios of litter are used; these ratios constitute indices of litter biodegradability, and each microbe releases appropriate enzymes related to the litter chemistry (Aerts, 1997; Carreiro *et al*., 2000; Kim, 2001). As litter is decomposed and becomes a part of soil OM, the quality of litter decreases because N-containing compounds are more biodegradable than recalcitrant materials such as lignin that are the last substances metabolized during litter degradation.

Types of plant species influence litter chemical composition because cellulose, hemicellulose, lignin and P contents in litter vary by species, tissue type, and maturity, and this composition affects biological degradation rates (Bertrand *et al*., 2006; Šnajdr *et al*., 2011). For example, degradation rates and EEa of litter residue were significantly different between two species in boreal peat land because of a difference in litter chemistry. In addition, Straková *et al*. (2011) reported that the impact of litter quality on EEa overruled the direct effect of water table drawdown on aerobic microbial activity. Thus, litter chemistry can be the strongest factor for regulating EEa, and can offset other physical and chemical properties in wetland soils.

Root exudation

Tree roots generally exude glucose, sucrose, fructose, carbohydrates, amino acids and oxygen by respiration (Grayston *et al*., 1996). Root exudation provided carbon sources to microbes and enhanced microbial and enzyme activities around the rhizosphere in salt marsh (Caravaca *et al*., 2005), constructed wetland (Huang *et al*., 2012; Korboulewsky *et al*., 2012; Salvato *et al*., 2012; Cui *et al*., 2013) and peat land soils (Kang and Freeman, 2007). However, when plants experience N deficit due to seedling plant, roots exude less asparagine, glutamine, and glycogen (Bowen, 1969), and thereby stimulate production of enzyme such as aspartase and glutaminase that are related to ammonia production.

The difference in vegetation types influences the population of microorganisms and respiration rates, and affects EEa. The results from a constructed wetland demonstrated that different emergent plant species influenced DOC concentrations, microbial growth and EEa of the rhizosphere (Kong *et al*., 2009; Salvato *et al*., 2012).

Limitation and Future Direction of EEa Research

Measurements of EEa have become an easy tool for investigating soil microbial responses in global climate change. Studies on the effects of global climate change have revealed that increased CO_2 influenced net primary productivity, species abundances, community compositions, and soil respiration rates in terrestrial ecosystems (Curtis and Wang, 1998; Zak *et al*., 2000). The enhanced primary productivity due to elevated CO_2 was reported to retard the litter decomposition rate (Cotrufo *et al*., 1994; Cotrufo and Ineson, 1995) and reduce EEa produced by the fungal community (Zheng *et al*., 2010) because it can change litter chemistry of plants, such as by increasing the content of tannins and of lignin in litter detritus. However, increased primary productivity increases the amount of root exudation from rhizosphere to soils, thereby stimulating enzyme activity related to limited nutrients and further increasing the CO_2 emission from soils due to enhanced heterotrophic soil respiration (Eversberger *et al*., 2001; Freeman *et al*., 2004). Besides increased CO_2 effect, anthropogenic N deposition that

mitigates the nutrient limitation and the water table drawdown that supplies oxygen to wetland soils can offset the negative effects of litter chemistry on EEa (Curtis *et al*., 1994; Gorissen *et al*., 1995; Arnone and Hirschel, 1997; Zheng *et al*., 2010). Thus, we need to more investigate how EEa production and OM decomposition rate are regulated by global climate change in order to predict how much CO_2 is emitted from wetland soils to atmosphere and how much organic carbon is accumulated in wetland soils (Burns *et al*., 2013). In addition, most of EEa researches of global climate change experiment are conducted under controlled conditions and thus, the EEa responses to global climate change must be examined under *in situ* conditions with the investigation of potential changes in plant and soil microbial communities (Henry, 2013).

One of the promising questions in EE researches is how EEa is associated with specific taxa and microbial populations and communities (Henry, 2013). For this research, genomic technique is used to investigate which gene sequences are produced for specific enzymes in complex microbial communities (Raes *et al*., 2007; Wilmes and Bond, 2008). The transcriptomic tools and proteomic methods are employed to examine controls on the expression of enzyme-coding genes and to detect which organisms produce the specific enzymes (Harrington *et al*., 2007; Wallenstein and Weintraub, 2008; Morozova *et al*., 2009). However, the genes using this research are not well conserved and have various alternated forms with the same functions (Kellner *et al*., 2007) and gene expression do not always guarantee the enzyme activities *in situ* conditions (Edwards *et al*., 2011). Thus, it needs to develop the multiple primers that detect a wide range of enzymes and the metagenomic approaches that do not require primers, and to consider other factors, such as enzyme persistence and turnover rate for interpreting the EEa in real environmental conditions.

Fungal ligninolytic enzymes can be used for maintaining the ecosystem services such as bioremediation, carbon sequestration and plant growth enhancement. For example, laccase and peroxidase produced from white-rot basidiomycete can be applied to degrade the persistent organic pollutants in wetland soils (Rao *et al.*, 2014; Kües, 2015). Many EE has been used for biosensor to monitor pollution (e.g. pesticides and heavy metals), stress conditions and management practices in various ecosystems (Morel *et al*., 2013; Rao *et al*., 2014). For these purposes, we need to know how we manipulate environments to promote specific gene expression and to enhance the microbial population and activity that generate the desired enzymes.

Summary and Conclusions

This article reviewed physical and chemical factors that affected EEa in wetland soils. Of the physical factors, the effects of pH, water table, and particle size of OM on EEa appeared to be similar among wetland soils, whereas temperature affected EEa differently depending on the acclimation of microbes to environmental conditions. The influence of C, N, and P on EEa was regulated by nutrient state, C:N ratios, limiting factors, and the types of EE in wetland soils. Specifically, in wetland soils, the quality of organic materials (substrate chemistry) was the most important of various regulators that affected EEa. Furthermore, global climate change can shift the frequency of drought, increase temperature, and decrease water table in wetlands. Global climate change and anthropogenic N deposition can influence the oxidative EEa and hydrolytic EEa, resulting in the change of CO_2 emission from wetland soils to the atmosphere. Thus the research on the relationship between microbial structure, EE functions and environmental factors controlling EEa can be applied to manipulate wetland ecosystems for treating pollutants and to monitor wetland ecosystem services.

적 요

육상과 수계의 전이지대에 위치한 습지는 빈번한 침수, 육상 생태계로부터의 영양염류의 유입, 수계와 토양에 적절하게 적응된 식생의 존재 및 토양 내 산소 결핍과 같은 독특한 특징을 가지고 있다. 이러한 생지화학적 특성과 독특한 식생의 존재는 유기물의 분해과정에 물리적·화학적 영향을 미치고 있는데, 특히 미생물에서 생산되는 체외효소 활성도는 유기물의 분해 과정과 관련을 맺고 있다. 체외효소는 고분자 유기물을 간단한 형태의 유기탄소, 무기 질소, 인, 황으로 분해하여 미생물과 식물이 용이하게 이들 영양물질을 흡수할 수 있도록 도움을 주기 때문에, 체외효소에 대한 연구는 습지 토양 내에서의 유기물 분해와 물질순환의 기작을 이해하는 데 필수적인 요소이다. 본 연

구는 습지 토양 내 β-glucosidase, β-N-acetylglucosaminidase, phosphatase, arylsulfatase, phenol oxidase와 같은 체외 효소 활성도에 영향을 미치는 물리적·생지화학적 요소가 무엇인지 문헌연구를 통하여 고찰하였다. 물리적 요소로써, pH 와 유기물의 입자 크기는 체외효소 활성도에 크게 영향을 미치지 않았으나, 온도에 대한 영향은 미생물의 극한 온도에서의 적응성 정도에 따라 다양하게 나타났다. 화학적 요소로써, 탄소, 질소, 인의 첨가는 습지 토양의 영양상태, C:N 비율과 제한 요소, 및 체외효소의 종류에 따라 그 영향이 다양하게 발현되었다. 특히, 유기물의 기질 특성(Substrate quality)은 다른 어떤 요소보다도 체외효소 활성도에 큰 영향을 미치는 것으로 나타났다. 향후 연구 과제로써는 기후 변화와 질소 침적의 증가에 따른 효소 활성도의 변화 및 분자생물학적 접근을 통한 미생물 군집과 체외효소 기능간의 관계를 규명하는 연구가 필요하다. 또한, 습지 토양내 체외효소 활성도를 극대화 할 수 있는 환경을 조성함으로써, 앞으로 습지 토양이 오염물질을 제거하고 습지의 생태학적 기능을 최대화 할 수 있는 연구가 요구된다.

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