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Review

Selected soil enzymes: Examples of their potential roles in the ecosystem

Joachim H. J. R. Makoi[1] and Patrick A. Ndakidemi[2*]

[1]Faculty of Applied Sciences, Cape Peninsula University of Technology, Cape Town Campus, Keizergracht, P.O. Box 652, Cape Town 8000, South Africa.
[2]Research and Technology Promotion, Cape Peninsula University of Technology, Cape Town Campus, Keizergracht, P.O. Box 652, Cape Town 8000, South Africa.

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Soil enzymes regulate ecosystem functioning and in particular play a key role in nutrient cycling. In this review we briefly summarise potential roles of selected enzymes such as amylase, arylsulphatases, β-glucosidase, cellulose, chitinase, dehydrogenase, phosphatase, protease and urease in the ecosystem. We also highlight areas where further research is needed to increase our understanding of other possible role(s) of enzymes and factors that may affect their activities in the ecosystem.

Key words: amylase, arylsulphatases, β-glucosidase, cellulose, chitinase, dehydrogenase, phosphatase, protease and urease.

INTRODUCTION

Soil enzymes play key biochemical functions in the overall process of organic matter decomposition in the soil system (Burns, 1983; Sinsabaugh et al., 1991). They are important in catalysing several important reactions necessary for the life processes of micro-organisms in soils and the stabilisation of soil structure, the decomposition of organic wastes, organic matter formation and nutrient cycling (Dick et al., 1994). These enzymes are constantly being synthesised, accumulated, inactivated and/or decomposed in the soil, hence playing an important role in agriculture and particularly in nutrients cycling (Tabatabai, 1994; Dick, 1997). The activities of these enzymes in soils undergo complex biochemical processes consisting of integrated and ecologically-connected synthetic processes, and in the immobilisation and enzyme stability (Khaziyev and Gulke, 1991). In this regard, all soils contain a group of enzymes that determine soil metabolic processes (McLaren, 1975) which, in turn, depend on its physical, chemical, microbiological and biochemical properties. The enzyme levels in soil systems vary in amounts primarily due to the fact that each soil type has different amounts of organic matter content, composition and activity of its living organisms and intensity of the biological processes (Stevenson, 1986). In practice, the biochemical reactions are brought about largely through the catalytic contribution of enzymes and variable sub-strates that serve as energy sources for micro-organisms (Kiss et al., 1978). These enzymes may include amylase, arylsulphatases, β-glucosidase, cellulose, chitinase, dehydrogenase, phosphatase, protease and urease released from plants (Miwa et al., 1937), animals (Kanfer et al., 1974), organic compounds and micro-organisms (Dick and Tabatabai, 1984; James et al., 1991; Richmond, 1991; Hans and Snivasan, 1969; Shawale and Sadana, 1981) and soils (Cooper, 1972; Gupta et al., 1993; Gareshamurthy et al., 1995).

A better understanding of the role of these soil enzymes activity in the ecosystem will potentially provide a unique opportunity for an integrated biological assessment of soils due to their crucial role in several soil biological activities, their ease of measurement, and their rapid response to changes in soil management practices (Dick, 1994; Dick, 1997; Bandick and Dick, 1999). Studies indicate that high enzyme activity signals mineral element limitation in the ecosystem (Sinsabaugh et al., 1993; Ndakidemi, 2006). Although there have been extensive studies on soil enzymes (Lizararo et al., 2005;

*Corresponding author. E-mail: NdakidemiP@cput.ac.za. Tel: +27214603128. Fax: +27214603887.

Mungai et al., 2005; Wirth and Wolf, 1992; Ross, 1976; Perucci and Scarponi, 1984), little has been reported on their roles in agricultural development. To better understand the roles of these enzymes' activity and efficiency, nine enzymes in soils were reviewed for agricultural development.

AMYLASE

Amylase is a starch hydrolysing enzyme (Ross, 1976). It is known to be constituted by α-amylase and β-amylase (Pazur, 1965; King, 1967; Thoma et al., 1971). Studies have shown that α-amylases are synthesised by plants, animals and micro-organisms, whereas, β-amylase is mainly synthesized by plants (Pazur, 1965; Thoma et al., 1971). This enzyme is widely distributed in plants and soils so it plays a significant role in the breakdown of starch. Research evidence suggests that several other enzymes are involved in the hydrolysis of starch, but of major importance are α-amylase which converts starch like substrates to glucose and/or oligosaccharides and β-amylase, which converts starch to maltose (Thoma et al., 1971).

Studies have, however, indicated that the roles and activities of α-amylase and β-amylase enzymes may be influenced by different factors ranging from cultural practices, type of vegetation, environment and soil types (Ross, 1968; Rose and Roberts, 1970; Pancholy and Rice, 1973; Rose, 1975a). For example, plants may influence the amylase enzyme activities of soil by directly supplying enzymes from their residues or excreted compounds, or indirectly providing substrates for the synthetic activities of micro-organisms. Greater understanding the role(s) and other chemical, biological, physical and agronomic factors influencing functioning of amylase enzymes in the soil will further define the significance of these enzymes in the soil, and enable proper management techniques to be devised to maximise the benefits that may be derived from such enzymes.

ARYLSULPHATASES

It has been established that sulphur uptake in plants is in the form of inorganic sulphate (SO_4) and its availability depends on its mineralisation or mobilisation (Williams, 1975; Fitzgerald, 1976) from aromatic sulphate esters (R-O-SO_3^-). This is due to the fact that certain proportions of sulphur in different soil profiles are bound into organic compounds and are indirectly available to plants. In this regard, its availability will depend on the extracellular hydrolysis of these aromatic sulphate esters or intracellular oxidation of soluble organic matter absorbed by the micro-organisms to yield energy and carbon skeletons for biosynthesis by which some SO_4-S are released as a by-product (Dodgson et al., 1982). All these processes are dependent on arylsuphatases enzymes (Stickland and Fitzgerald, 1984; Fitzgerald and Stickland, 1987). Arylsulphatases are typically widespread in nature (Dodgson et al., 1982) as well as in soils (Tabatabai and Bremner, 1790a, b; Cooper, 1972; Spier et al., 1980; Gupta et al., 1993; Ganeshamurthy et al., 1995). They are responsible for the hydrolysis of sulphate esters in the soil (Kertesz and Mirleau, 2004) and are secreted by bacteria into the external environment as a response to sulphur limitation (McGill and Colle, 1981). Its occurrence in different soil systems is often correlated with microbial biomass and rate of S immobilisation (Klose et al., 1999; Klose and Tabatabai, 1999; Vong et al., 2003). The role of this enzyme in the hydrolysis of aromatic sulphate esters (R-O-SO_3^-) to phenols (R-OH) and sulphate, or sulphate sulphur (SO_4^{-2} or SO4-S) is shown in the following simple chemical equation (Spencer, 1958; Tabatabai, 1994):

$$R-O-SO_3^- \xrightarrow[Arylsulphatases]{Hydrolysis} R-OH + SO_4^{-2}$$

Studies have shown that the release of sulphate from soluble and insoluble sulphate esters in the soil is affected by various environmental factors (Burns, 1982) such as heavy metal pollution (Tyler, 1981); pH changes in the soil solution (Acosta-Martinez and Tabatabai, 2000); organic matter content and its type (Tabatabai and Bremner, 1971; Ladd, 1978; Sarathchandra and Perrott, 1981; Dalal, 1982); the concentration of organic sulphate esters (Dogson and Rose, 1976); the extent to which organic sulphate esters are protected against enzymatic hydrolysis such as sorption to particles surfaces in soils, and the activity persistence of extracellular arylsulphatases in the soil.

Considering the importance of S in plant nutrition, a better understanding of the role(s) of arylsulphatases in S mobilisation in agricultural soils is critical. So far, very little is known about specific microbial genera or species that play an important role in the soil organosulphur circle (Kertesz and Mirleau, 2004) in which arylsulphatases is the key enzyme. Researchers may also establish other unknown factors that affect activities of these enzymes in the ecosystem.

β-GLUCOSIDASE

β-glucosidase is a common and predominant enzyme in soils (Eivazi and Tabatabai, 1988; Tabatabai, 1994). It is named according to the type of bond that it hydrolyses. This enzyme plays an important role in soils because it is involved in catalysing the hydrolysis and biodegradation of various β-glucosides present in plant debris decomposing in the ecosystem (Ajwa and Tabatabai, 1994; Martinez and Tabatabai, 1997). Its final product is glucose, an important C energy source of life to microbes in the soil (Esen, 1993). There is considerable evidence

suggesting that a significant fraction of enzyme activity measured in soil originates from abiontic enzymes (enzymes of biological origin no longer associated with living cells) excreted into the soil solution or immobilised enzymes of microbial origin sorbed to clays or humic colloids (Skujins, 1976; Hayano and Katami, 1977; Busto and Perez-Mateos, 1995; 2000; Hayano and Tubaki, 1985; Hopes and Burns, 1987).

β-glucosidase is characteristically useful as a soil quality indicator, and may give a reflection of past biological activity, the capacity of soil to stabilise the soil organic matter, and can be used to detect management effect on soils (Bandick and Dick, 1999; Ndiaye et al., 2000). This has greatly facilitated its adoption for soil quality testing (Bandick and Dick, 1999). Generally, β-glucosidase activities can provide advanced evidence of changes in organic carbon long before it can be accurately measured by other routine methods (Dick, 1994; Dick et al., 1996; Wick et al., 1998). Several researchers have however also reported its phytopathological effects in the ecosystem (Davis et al., 1953; Sherrod and Domsch, 1970; Melouk and Horner, 1973). For example, some of the aglycons are known to be the precursors of the toxic substances which cause soil sickness where plants are grown as monocrops (Patrick, 1955; Borner, 1958).

β-glucosidase enzyme is very sensitive to changes in pH, and soil management practices (Dick et al., 1996; Acosta-Martinez and Tabatabai, 2000; Kuperman and Carreiro, 1997; Bergstrom et al., 1998; Leiros et al., 1999; Bandick and Dick, 1999; Madejon et al., 2001). Acosta-Martinez and Tabatabai (2000) reported β-glucosidase as sensitive to pH changes. This property can be used as a good biochemical indicator for measuring ecological changes resulting from soil acidification in situations involving activities of this enzyme. β-glucosidase enzyme is also known to be inhibited by heavy metal contamination such as Cu and several others (Haanstra and Doelman, 1991; Deng and Tabatabai, 1995; Wenzel et al., 1995). For instance, studies have shown that plant debris did not decomposed or show β-glucosidase activities when exposed to heavy metal polluted soils (Watson et al., 1976; Geiger et al., 1993). Consequently, more understanding of the β-glucosidase enzyme activities and factors influencing them in the ecosystem may contribute significantly to soil health studies.

CELLULASES

Cellulose is the most abundant organic compound in the biosphere, comprising almost 50% of the biomass synthesised by photosynthetic fixation of CO_2 (Eriksson et al., 1990). Growth and survival of micro-organisms important in most agricultural soils depends on the carbon source contained in the cellulose occurring in the soils (Deng and Tabatabai, 1994). However, for carbon to be released as an energy source for use by the micro-organisms, cellulose in plant debris has to be degraded into glucose, cellobiose and high molecular weight oligosaccharides by cellulases enzymes (White, 1982). Cellulases are a group of enzymes that catalyse the degradation of cellulose, polysaccharides build up of β-1, 4 linked glucose units (Deng and Tabatabai, 1994). It has been reported that cellulases in soils are derived mainly from plant debris incorporated into the soil, and that a limited amount may also originate from fungi and bacteria in soils (Richmond, 1991). Currently, it is generally accepted that the cellulases system comprises of three major types of enzymes. They include: endo-1, 4- β-glucanase which attacks the cellulose chains at random, exo-1, 4- β-glucanase which removes glucose or cellobiose from the non-reducing end of the cellulose chains, and β-D-glucosidase which hydrolyses cellobiose and other water soluble cellodextrins to glucose. Previously, several hypotheses were proposed about the mechanisms involved in the degradation of cellulose by the cellulases (Rees et al., 1950; Rees, 1975; White, 1982; Wood, 1991) although none of them has been fully accepted.

Demonstrating the effects of increasing concentrations of fungicides on cellulases activities, Petkar and Rai (1992) showed that there was a decreasing effect with fungicides captan, cosan, thiram, zinels and sandolex. More recently, Arinze and Yubedee (2000) reported that fungicides benlate, calixin and captan inhibited cellulase activity in *Fusarium monoliforme* isolates. Captatol inhibited cellulose activity in the sandy loam soil (Atlas et al., 1978), and chlorothalonil showed a clear reduction in cellulase activity under flooded or non-flooded conditions (Vicent and Sisler, 1968).

Studies have shown that activities of cellulases in agricultural soils are affected by several factors. These include temperature, soil pH, water and oxygen contents (abiotic conditions), the chemical structure of organic matter and its location in the soil profile horizon (Rubidge, 1977; Gomah, 1980; Tabatabai, 1982; Klein, 1989; Deng and Tabatabai, 1994; Alf and Nannipieri, 1995), quality of organic matter/plant debris and soil mineral elements (Burns, 1978; Hope and Burns, 1987; Klein, 1989; Sinsabaugh and Linkins, 1989; Deng and Tabatabai, 1994) and the trace elements from fungicides (Deng and Tabatabai, 1994; Petkar and Rai, 1992; Arinze and Yubedee 2000; Atlas et al., 1978; Vicent and Sisler, 1968). Srinivasulu and Rangaswamy (2006) reported a significantly more stimulatory effect of cellulases in black soil than red soil. Several mechanisms have been proposed in the degradation of cellulose by cellulases (Rees et al., 1950; Rees, 1975; White, 1982, Wood, 1991). For instance, chitin in the presence of cellulose induces the synthesis of chitinase and other cell wall lytic enzymes which promote the release of the intramural β-glucosidase into the medium. All these findings suggest that activities of cellulases can be used to give preliminary indication of some of the physical chemical pro-

perties of soil, thus, easing agricultural soil management strategies. Since cellulases enzymes play an important role in global recycling of the most abundant polymer, cellulose in nature, it would be of critical importance to understand this enzyme better so that it may be used more regularly as a predictive tool in our soil fertility programmes. More information on the role of this enzyme is needed since it is affected by different factors which may jeopardise its involvement in the decomposition of cellulolytic materials in the soil for microbial use and improved soil health in agricultural ecosystems.

CHITINASE

Chitinase or chitinolytic enzymes are key enzymes responsible for the degradation and hydrolysis of chitin (poly β-1-4-(2-ncetamido-2-deoxy)-D-glucoside). They are also considered as the major structural component of many fungal cell walls that use the hyperparasitism mechanisms against pests/pathogen attack, (Bartinicki-Garcia, 1968; Chet and Henis, 1969; Chet and Henis, l975; Chet, 1987). These biological agents also reduce disease producing agents by using other mechanisms such as antibiosis or competition mechanisms (Parl, 1960). This agriculturally important enzyme is produced or released by various organisms including plants and micro-organisms (Deshpande, 1986). For example, in plants, the chitinase enzyme is induced and accumulated in response to microbial infections and it is thought to be involved in the defence of plants against pathogen infections (Boiler et al., 1983; Boiler, 1985). Its presence in different forms in the ecosystem has demonstrated its effectiveness in the control of soil-borne diseases such as *Sclerotium rolfsii* and *Rhizoctonia solani* in beans and cotton, respectively (Ordentlich et al., 1988; Shapira et al., 1989). Biological control of damping off caused by *R. solani* was achieved by applying antagonistic fungi and bacteria isolated from coastal soils with chitinase activities (Ordentlich et al., 1988; Gal, 1992; Tweddel et al. 1994). One of the mechanisms proposed involves lytic enzymes that cause the degradation of cell walls of pathogenic fungi (Sneh, 1981; Elad et al., 1982; Hadar et al., 1983; Ordentlich et al, 1988; Chet et al., 1990; Singh et al., 1999). As biological control of most pathogenic diseases is increasingly gaining popularity in recent times due to their environmental friendliness, better understanding of the chitinolytic enzymes is likely to uncover more application avenues for this enzyme in agricultural systems and, consequently, increase plant growth and final yields.

DEHYDROGENASE

The dehydrogenase enzyme activity is commonly used as an indicator of biological activity in soils (Burns, 1978). This enzyme is considered to exist as an integral part of intact cells but does not accumulate extracellularly in the soil. Dehydrogenase enzyme is known to oxidise soil organic matter by transferring protons and electrons from substrates to acceptors. These processes are part of respiration pathways of soil micro-organisms and are closely related to the type of soil and soil air-water conditions (Doelman and Haanstra, 1979; Kandeler et al., 1996; Glinski and Stepniewski, 1985). Since these processes are part of respiration pathways of soil micro-organisms, studies on the activities of dehydrogenase enzyme in the soil is very important as it may give indications of the potential of the soil to support biochemical processes which are essential for maintaining soil fertility.

With regard to soil air-water relationships, studies have shown that dehydrogenase enzyme was greater in flooded compared to non-flooded soil (Dkhar and Mishra, 1983; Baruah and Mishra, 1984; Benckiser et al., 1984; Tiwari et al., 1989). The increase in this enzyme after flooding was also related to decreased redox potential (Okazaki et al., 1983; Pedrazzini and McKee, 1984). A study by Brzezinska et al. (1998) suggested that soil water content and temperature influence dehydrogenase activity indirectly by affecting the soil redox status.

After flooding the soil, oxygen present is rapidly exhausted so that a shift of the activity from aerobic to anaerobic micro-organisms takes place. Such redox transformations are closely connected with respiration activity of soil micro-organisms. They may serve as indicators of the microbiological redox systems in soils and can be considered a possible measure of microbial oxidative activity (Glinski and Stepniewski, 1985; Gunnison, et al., 1985; Skujins, 1973; Casida, 1977; Tabatabai, 1982; Trevors, 1984). The relationship between dehydrogenase activity and redox potential (Eh) as well as Fe^{2+} content may also be used to illustrate the reactions of soil micro-organisms to the changes in soil environment. For instance, lack of oxygen may trigger facultative anaerobes to initiate metabolic processes involving dehydrogenase activities and the use of Fe (III) forms as terminal electron acceptors (Bromfield, 1954, Galstian, 1974), a process that may affect iron availability to plants in the ecosystem (Benckiser et. al., 1984). Some studies have shown that reducing conditions in the soil were associated with high Fe^{2+} concentration in the soil solution and a significant increase of extra plasmatic Fe in roots of maize due to intense stimulation of microbial growth and dehydrogenase activities in the ecosystem (Fiedler et. al., 2004).

Additionally, dehydrogenase enzyme is often used as a measure of any disruption caused by pesticides, trace elements or management practices to the soil (Reddy and Faza, 1989; Wilke, 1991; Frank and Malkomes, 1993), as well as a direct measure of soil microbial activity (Skujins, 1978; Trevors, 1984; Garcia and Hernandez, 1997). It can also indicate the type and significance of pollution in soils. For example, dehydroge-

nase enzyme is high in soils polluted with pulp and paper mill effluents (McCarthy et al., 1994) but low in soils polluted with fly ash (Pitchel and Hayes, 1990). Similarly, higher activities of dehydrogenases have been reported at low doses of pesticides, and, lower activities of the enzyme at higher doses of pesticides (Baruah and Mishra, 1986). As most areas of the world are often polluted by different industrial bio-chemical products, better understanding of the role of this enzyme in environmental science will open greater possibilities of using it as a diagnostic tool for better ecosystem assessment and amelioration.

PHOSPHATASES

Phosphatases are a broad group of enzymes that are capable of catalysing hydrolysis of esters and anhydrides of phosphoric acid (Schmidt and Lawoski 1961). In soil ecosystems, these enzymes are believed to play critical roles in P cycles (Speir and Ross, 1978) as evidence shows that they are correlated to P stress and plant growth. Apart from being good indicators of soil fertility, phosphatase enzymes play key roles in the soil system (Dick and Tabatai, 1992; Eivazi and Tabatabai, 1997; Dick et al., 2000).

Land plants have evolved many morphological and enzymatic adaptations to tolerate low phosphate availability. This includes transcription activity of acid phosphatases, which tend to increase with high P stress (Tarafdar and Jungk, 1987; Goldstein, 1992; Duff et al., 1994; del Pozo et al., 1999; Haran et al., 2000; Baldwin et al., 2001; Miller et al., 2001; Li et al., 2002). For example, when there is a signal indicating P deficiency in the soil, acid phosphatase secretion from plant roots is increased to enhance the solubilisation and remobilisation of phosphate, thus influencing the ability of the plant to cope with P-stressed conditions (Muchhal et al., 1996; Daram et al., 1999; Kai et al., 2002; Karthikeyan et al., 2002; Mudge et al., 2002; Versaw and Harrison, 2002; Nakas et al., 1987; Chrost, 1991; Hayes et al., 1999; Li et al., 1997).

The amount of acid phosphatase exuded by plant roots has been shown to differ between crop species and varieties, (Ndakidemi, 2006; Izaguirre-Mayoral and Carballo, 2002) as well as crop management practices (Ndakidemi, 2006; Patra et al., 1990; Staddon et al., 1998; Wright and Reddy, 2001). For instance, research has shown that legumes secrete more phosphatase enzymes than cereal (Yadav and Tarafdar, 2001). This may probably be due to a higher requirement of P by legumes in the symbiotic nitrogen fixation process as compared to cereals. In their studies, Li et al. (2004) reported that chickpea roots were also able to secrete greater amounts of acid phosphatase than maize.

The ability to solubilise soil mineral elements by these phosphomonoesteraces is expected to be a higher in biologically-managed systems because of a higher quantity of organic C found in those systems. In fact, the activity of acid and alkaline phosphatases was found to correlate with organic matter in various studies (Guan 1989; Jordan and Kremer, 1994; Aon and Colaneri, 2001). Another factor that influences the rate of synthesis, release and stability of this enzyme is the soil pH (Eivazi and Tabatabai, 1977; Juma and Tabatabai, 1977; Tabatabai, 1994; Martínez and Tabatabai, 2000). For example, phosphomonoesteraces inducibility and their exudation intensity by plant roots and micro-organisms are determined by their orthophosphate need, which is in turn affected by soil pH (Skujins, 1976). It is, therefore, anticipated that management practices that induce P stress in the rhizosphere may also affect the secretion of these enzymes in the ecosystem (Ndakidemi, 2006).

To date, there have been few studies examining the influence of management options in the ecosystem on phosphatases activity in soil where most crops are grown. Understanding the dynamics of enzyme activities in these systems is crucial for predicting their interactions as their activities may, in turn, regulate nutrient uptake and plant growth.

PROTEASE

Proteases in soil play a significant role in N mineralisation (Ladd and Jackson, 1982), an important process regulating the amount of plant available N (Stevenson, 1986) and plant growth. This enzyme in the soil is generally associated with inorganic and organic colloids (Burns, 1982; Nannipieri et al., 1996). Protease activities have been reported to occur partly in soil as a humo-carbohydrate complex (Mayaudon et al., 1975; Batistic et al., 1980) from arable soil (Ladd, 1972; Mayaudon et al., 1975; Hayano et al., 1987); from solid municipal waste compost (Rad et al., 1995), and from forest or permanent grassland soils (Nannipieri et al., 1980, 1982, 1985). The amount of this extracellular enzyme activity may be indicative not only of the biological capacity of soil for the enzymatic conversion of the substrate, which is independent of the extent of microbial activity, but might also have an important role in the ecology of micro-organisms in the ecosystem (Burns, 1982).

Protease activities are affected by several biotic and abiotic factors. For example, low concentrations of neutralised soil humic acids (l-100 pg mL^{-1}) inhibit some and stimulate other protease activity by mechanisms involving primarily humic acid carboxyl groups (Ladd and Butler, 1969a, b; Butler and Ladd, 1969b). The enzyme pronase is inhibited irrespective of the charge of the substrate hydrolysed, suggesting that decreased activity results from humic acid combining with enzyme rather than with substrate (Ladd and Butler, 1969b). Furthermore, quantitative considerations of the effects of humic acid and substrate concentrations on pronase hydrolysis

of carbobenzoxy-glycyl leucine indicates that inhibition is not due to the combination of humic acid and substrate anions (Ladd and Butler, 1969a).

There is a need to study the properties and factors affecting naturally-occurring enzyme complexes such as those involving protease enzymes in the soil ecosystem as they may reveal some unknown role(s) in soil fertility management.

UREASE

Urease enzyme is responsible for the hydrolysis of urea fertiliser applied to the soil into NH_3 and CO_2 with the concomitant rise in soil pH (Andrews et al., 1989; Byrnes and Amberger, 1989). This, in turn, results in a rapid N loss to the atmosphere through NH_3 volatilisation (Fillery et al., 1984; Simpson et al., 1984, 1985; Simpson and Freney, 1988). Due to this role, urease activities in soils have received a lot of attention since it was first reported by Rotini (1935), a process considered vital in the regulation of N supply to plants after urea fertilisation.

Often, urea is the main source of N in many crops including flooded or irrigated rice and maize in many parts of Africa and Asia (Stangel, 1984; Buresh et al., 1988; Byrnes and Amberger, 1989; Van Cleemput and Wang, 1991). Despite the importance of this fertiliser, its efficiency has been reported as low (Mikkelsen et al., 1978; Fillery et al., 1986; Vlek and Byrnes, 1986) due to substantial N lost to the atmosphere through volatilisation, a process mediated by the urease enzyme (Fillery et al., 1984; Simpson et al., 1984, 1985; Simpson and Freney, 1988; Byrnes and Amberger, 1989).

Soil urease originates mainly from plants (Polacco, 1977) and micro-organisms found as both intra- and extra-cellular enzymes (Mulvaney and Bremner, 1981; Blakeley and Zerner, 1984; Burns, 1986; Mobley and Hausinger, 1989). The stability of this enzyme in the system is affected by several factors. For example, studies have shown that extracellular urease associated with soil organo-mineral complexes is more stable than urease in the soil solution (Burns, 1986) and those humus-urease complexes extracted from soil are highly resistant to denaturing agents such as extreme temperatures and proteolytic attack (Nannipieri et al., 1978). On the other hand, urease extracted from plants or micro-organisms is rapidly degraded in soil by proteolytic enzymes (Burns et al., 1972a; Pettit et al., 1976; Zantua and Bremner, 1977). This suggests that a significant fraction of ureolytic activity in soil is carried out by extracellular urease, which is stabilised by immobilisation on organic and mineral soil colloids.

Urease activity in soils is influenced by many factors. These include cropping history, organic matter content of the soil, soil depth, soil amendments, heavy metals, and environmental factors such as temperatures (Tabatabai, 1977; Bremner and Mulvaney, 1978; Yang et al., 2006). For example, studies have shown that urease was very sensitive to toxic concentrations of heavy metals (Yang et al., 2006). Other studies with soil samples taken from horizons of different soil profiles revealed decreased activities with increased soil depth. The differences were attributed to decreases in soil organic matter content with depth (Hoffmann, 1959; Myers and McGarity, 1968; Ross and Roberts, 1968; Skujins, 1967). The effect of temperature on urea hydrolysis has received considerable research attention (Gould et al., 1973; Dalal, 1975; Bremner and Mulvaney, 1978; Tomar and Mackenzie, 1984; Kissel and Cabrera, 1988). Generally, urease activity increases with increasing temperature. It is suggested that higher temperatures increase the activity coefficient of this enzyme. Therefore, it is recommended that urea be applied at times of the day when temperatures are low. This is because during such times the activation energy is low, thus, resulting in minimum loss of N by the volatilisation process.

Since urease plays a vital role in the hydrolysis of urea fertiliser, it is important to uncover other unknown factors that may reduce the efficiency of this enzyme in the ecosystem. A better understanding of this enzyme would provide more effective ways of managing urea fertiliser especially in high rainfall areas, flooded soils and irrigated lands as well as where urea fertiliser is vulnerable to urease enzyme.

CONCLUSION

Understanding other possible roles of soil enzymes is vital to soil health and fertility management in ecosystems. These enzymes may have significant effects on soil biology, environmental management, growth and nutrient uptake in plants growing in ecosystems. Their activities may, however, be influenced by unknown cultural management practices. Research efforts should focus on discovering new enzymes from microbial diversity in the soil, the most appropriate practices that may positively influence their activities for improved plant growth as well as improving the biological environments in order to sustain sustain other life types.

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