

Review

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

Joachim H. J. R. Makoi¹ and Patrick A. Ndakidemi^{2*}

¹Faculty of Applied Sciences, Cape Peninsula University of Technology, Cape Town Campus, Keizergracht, P.O. Box 652, Cape Town 8000, South Africa.

²Research and Technology Promotion, Cape Peninsula University of Technology, Cape Town Campus, Keizergracht, P.O. Box 652, Cape Town 8000, South Africa.

Accepted 30 January, 2008

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

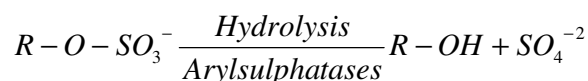
Amylase is a starch hydrolysing enzyme (Ross, 1976). It is known to be constituted by α -amylase and β -amylase (Pazur, 1965; King, 1967; Thoma et al., 1971). Studies have shown that α -amylases are synthesised by plants, animals and micro-organisms, whereas, β -amylase is mainly synthesized by plants (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 arylsulphatases 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, 1970a, 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 SO_4-S) is shown in the following simple chemical equation (Spencer, 1958; Tabatabai, 1994):



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 (Dodgson 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 abiotic 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 CO₂ (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 cellobioses 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 moniliforme* isolates. Captatol inhibited cellulase 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-

properties 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-nacetamido-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, (Bartnicki-Garcia, 1968; Chet and Henis, 1969; Chet and Henis, 1975; 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 Tabatabai, 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 phosphomonoesterases 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, phosphomonoesterases 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 (1-100 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 other life types.

ACKNOWLEDGEMENT

This study was supported by the Cape Peninsula University of Technology through University Research Funds 2007/RP03.

REFERENCES

- Acosta-Martínez V, Tabatabai MA (2000). Enzyme activities in a limed agricultural soil. *Biol. Fert. Soils* 31: 85-91.
- Ajwa HA, Tabatabai MA (1994). Decomposition of different organic materials in soils. *Biol. Fert. Soils* 18: 175-182.
- Alf K, Nannipieri P (1995). Cellulase activity, *Methods in Applied Soil Microbiology and Biochemistry*, Academic Press, London.
- Andrews RK, Blakeley RL, Zerner B (1989). Urease: A Ni (II) metalloenzyme. In *The Bioinorganic Chemistry of Nickel*, ed. J. R. Lancaster, pp. 141-166. VCH Publishers, New York.

- Aon MA, Colaneri AC (2001). Temporal and spatial evolution of enzymatic activities and physico-chemical properties in an agricultural soil. *Appl. Soil Ecol.* 18: 255-270.
- Arinze AE, Yubedee AG (2000). Effect of fungicides on *Fusarium* grain rot and enzyme production in maize (*Zea mays* L.). *Glob. J. Appl. Sci.* 6(4): 629-634.
- Atlas RM, Pramer D, Bartha R (1978). Assessment of pesticide effects on non-target soil microorganisms. *Soil Biol. Biochem.* 10: 231-239.
- Baldwin JC, Karthikeyan AS, Raghothama KG (2001). LEPS2, a phosphorus starvation-induced novel acid phosphatase from tomato. *Plant Physiol.* 125: 728-737.
- Bandick AK, Dick RP (1999). Field management effects on soil enzyme activities. *Soil Biol. Biochem.* 31:1471-1479.
- Bartinicki-Garcia S (1968). Cell wall chemistry, morphogenesis and taxonomy of fungi. *Ann. Rev. Microbiol.* 144: 346-349.
- Baruah M, Mishra RR (1984). Dehydrogenase and urease activities in rice field soils. *Soil Biol. Biochem.* 16: 423-424.
- Baruah M, Mishra RR (1986). Effect of herbicides butachlor, 2,4-d and oxyfluorfen on enzyme activities and CO₂ evolution in submerged paddy field soil. *Plant Soil* 96: 287-291.
- Batistic L, Sarkar JM, Mayaudon J (1980). Extraction, purification and properties of soil hydrolases. *Soil Biol. Biochem.* 12: 59-63.
- Benckiser G, Santiago S, Neue HU, Watanabe I, Ottow JCG (1984). Effect of fertilization and exudation, dehydrogenase activity, iron-reducing populations and Fe²⁺ formation in the rhizosphere of rice (*Oryza sativa* L.) in relation to iron toxicity. *Plant Soil* 79: 305-316.
- Bergstrom DW, Monreal CM, King DJ (1998). Sensitivity of soil enzyme activities to conservation practices. *SSSAJ* 62: 1286-1295.
- Blakeley RL, Zerner B (1984). Jack bean urease: the first nickel enzyme. *J. Mol. Catal.* 23: 263-292.
- Boiler T (1985). Induction of hydrolases as a defense reaction against pathogens. In: *Cellular and Molecular Biology of Plum Stress* (Key JL, Kosuge T Eds.) pp. 247-262. Liss. New York.
- Boiler T, Gehri A, Mauch F, Vogeli U (1983). Chitinase in bean leaves: induction by ethylene, purification, properties and possible function. *Planta.* 157: 22-31.
- Borner H (1958). Untersuchungen über den Abbau von Phlorizin im Boden. Ein Beitrag zum Problem der Bodenmüdigkeit bei Obstgehölzen. *Naturwiss.* 45: 138-139.
- Bremner JM, Mulvaney RL (1978). Urease activity in soils. In: *Soil Enzymes* (Burns RG, Ed.), pp 149-196. Academic Press, London.
- Bromfield SM (1954). Reduction of ferric compounds by soil bacteria. *J. Gen. Microbiol.* 11: 1-6.
- Brzezinska M, Stepniewska Z, Stepniewski W (1998). Soil oxygen status and dehydrogenase activity. *Soil Biol. Biochem.* 30(13): 1783-1790.
- Buresh RJ, De Datta SK, Padilla JL, Samson MI (1988). Effect of two urease inhibitors on floodwater ammonia following urea application to lowland rice. *SSSAJ* 52: 856-861.
- Burns RG (1978). Enzyme activity in soil: Some theoretical and practical considerations. In: *Soil Enzymes* (Burns RG, Ed.), pp. 295-340. Academic Press, London.
- Burns RG (1978). *Soil Enzymes*. Academic Press, New York, p. 370.
- Burns RG (1982). Enzyme activity in soil: location and possible role in microbial ecology. *Soil Biol. Biochem.* 14: 423-427.
- Burns RG (1983). Extracellular enzyme-substrate interactions in soil. In: *Microbes in Their Natural Environment* (Slater JH, Wittenbury R and Wimpenny JWT Eds), pp. 249-298. Cambridge University Press, London.
- Burns RG (1986). Interaction of enzymes with soil mineral and organic colloids. In: *Interactions of Soil Minerals with Natural Organics and Microbes*, ed. (Huang PM, Schnitzer M Eds), Soil Sci. Soc. Am. Madison, pp. 429-452.
- Burns RG, Pukite AH, McLaren AD (1972a). Concerning the location and persistence of soil urease. *SSSAP* 36: 308-311.
- Busto MD, Perez-Mateos M (1995). Extraction of humic-β-glucosidase fractions from soil. *Biol. Fert. Soils* 20: 77-82.
- Busto MD, Perez-Mateos M (2000). Characterisation of β-D-glucosidase extracted from soil fractions. *Eur. J. Soil Sci.* 51:193-200.
- Butler JHA, Ladd JN (1969). The effect of methylation of humic acids on their influence on proteolytic enzyme activity. *Austr. J. Soil Res.* 7: 263-268.
- Byrnes BH, Amberger A (1989). Fate of broadcast urea in a flooded soil when treated with N-(n-butyl)thiophosphoric triamide, a urease inhibitor. *Fertil. Res.* 18: 221-231.
- Casida LE Jr (1977). Microbial metabolic activity in soil as measured by dehydrogenase determinations. *Appl. Environ. Microbiol.* 34: 630-636.
- Chet I (1987). Trichoderma-application, mode of action, and potential as biocontrol agent of soil borne pathogenic fungi. In: Chet I (Ed.) *Innovative approaches to plant disease control*, Wiley, New York, pp. 137-349.
- Chet I, Henis Y (1969). Effect of catechol and disodium EDTA on melanin content of hyphal and sclerotial walls of *Sclerotium rolfsii* Sacc. and the role of melanin in the susceptibility of these walls to β-1-3 glucanase and chitinase. *Soil Biol. Biochem.* 1: 131-138.
- Chet I, Henis Y (1975). Sclerotial morphogenesis in fungi. *Ann. Rev. Phytopathol.* 13: 169-192.
- Chet I, Ordentlich A, Shapira R, Oppenheim A (1990). Mechanism of biocontrol of soil borne plant pathogen by rhizobacteria. *Plant Soil.* 129: 85-92.
- Chrost RJ (1991). *Microbial enzymes in aquatic environments*. Springer-Verlag, New York, USA.
- Cooper PJM (1972). Arylsulphatase activity in Northern Nigerian soils. *Soil Biol. Biochem.* 4: 333-337.
- Dalal RC (1975). Urease activity in some Trinidad soils. *Soil Biol. Biochem.* 7: 5-8.
- Dalal RC (1982). Effect of plant growth and addition of plant residues on the phosphatase activity in soil. *Plant Soil.* 66: 265-269.
- Daram P, Brunner S, Rausch C, Steiner C, Amrhein N, Bucher M (1999). Pht2: I encodes a low affinity phosphate transporter from *Arabidopsis*. *Plant Cell* 11: 2153-2166.
- Davis D, Waggoner PE, Dimond AE (1953). Conjugated phenols in the *Fusarium wilt* syndrome. *Nature, Lond.* 172: 959-961.
- del Pozo JC, Allona I, Rubio V, Layva A, de la Pena A, Aragoncillo C, Paz-Area J (1999). A type 5 acid phosphatase gene from *Arabidopsis thaliana* is induced by phosphate starvation and by some other types of phosphate mobilizing/oxidative stress conditions. *Plant J.* 19: 579-589.
- Deng SP, Tabatabai MA (1994). Cellulase activity of soils. *Soil Biol. Biochem.* 26: 1347-1354.
- Deng SP, Tabatabai MA (1995). Cellulase activity of soils: effect of trace elements. *Soil Biol. Biochem.* 27(7): 977-979.
- Deshpande MV (1986). Enzymatic degradation of chitin and its biological applications. *J. Sci. Ind. Res.* 45: 273-281.
- Dick RP (1994). Soil enzyme activities as indicators of soil quality. In: Doran JV, Coleman DC, Bezdicek DF, Stewart BA (Eds.). *Defining Soil Quality for a Sustainable Environment*, Soil Science Society of America, American Society of Agriculture, Madison, pp. 107-124.
- Dick RP (1997). Soil enzyme activities as integrative indicators of soil health. In: Pankhurst CE, Doube BM, Gupta VVSR (Eds.). *Biological Indicators of Soil Health*, CAB International, Wellingford, pp. 121-156.
- Dick RP, Breakwell DP, Turco RF (1996). Soil enzyme activities and biodiversity measurements as integrative microbiological indicators. In: *Methods for Assessing Soil Quality*, vol. 9. Soil Sci. Soc. Am. Madison, WI pp. 9-17.
- Dick RP, Sandor JA, Eash NS (1994). Soil enzyme activities after 1500 years of terrace agriculture in the Colca Valley, Peru. *Agric. Ecosyst. Environ.* 50: 123-131.
- Dick WA, Cheng L, Wang P (2000). Soil acid and alkaline phosphatase activity as pH adjustment indicators. *Soil Biol. Biochem.* 32: 1915-1919.
- Dick WA, Tabatabai MA (1984). Kinetic parameters of phosphatase in soils and organic waste materials. *Soil Sci.* 137: 7-15.
- Dick WA, Tabatai MA (1992). Potential uses of soil enzymes. In: Metting FB Jr. (Ed.), *Soil Microbial Ecology: Applications in Agricultural and Environmental Management*, Marcel Dekker, New York, pp. 95-127.
- Dkhar MS, Mishra RR (1983). Dehydrogenase and urease activities of maize (*Zea mays* L.) field soils. *Plant Soil* 70: 327-333.
- Dodgson KS, Rose FA (1976). Sulfohydrolases. In: *Metabolism of Sulfur Compounds Vol. 7, Metabolic Pathways* (Greenberg DM. Ed.), pp. 359-431. Academic Press, London.
- Dodgson KS, White G, Fitzgerald JW (1982). *Sulphatase Enzyme of Microbial Origin*, Vol. I. CRC Press, Florida.

- Doelman P, Haanstra L (1979). Effect of lead on soil respiration and dehydrogenase activity. *Soil Biol. Biochem.* 11: 475-479.
- Duff SMG, Sarath G, Plaxton WC (1994). The role of acid phosphatases in plant phosphorus metabolism. *Physiol. Plant.* 90: 791-800.
- Eivazi F, Tabatabai MA (1977). Phosphates in soils. *Soil Biol. Biochem.* 9: 167-172.
- Eivazi F, Tabatabai MA (1988). Glucosidases and galactosidases in soils. *Soil Biol. Biochem.* 20: 601-606.
- Elad Y, Chet I, Henis Y (1982). Degradation of plant pathogenic fungi by *Trichoderma harzianum*. *Can. J. Microbiol.*, 28: 719-725.
- Eriksson KEL, Blanchette RA, Ander P (1990). Biodegradation of cellulose. In: *Microbial and Enzymatic Degradation of Wood and Wood Components* (Eriksson KEL, Blanchette RA, Ander P. Eds.), pp. 89-180. Springer-Verlag, New York.
- Esen A (1993). β -glucosidases: overview. In: Esen A (Ed.) β -glucosidases and molecular biology. American Chemical Society, Washington, DC, pp. 9-17.
- Esen A (1993). β -Glucosidases-Biochemistry and Molecular Biology, ACS Symposium Series, 533, American Chemical Society, Washington, D. C.
- Fiedler S, Strasser O, Neumann G, Römheld V (2004). The influence of redox conditions in soils on extraplasmatic Fe-loading of plant roots. *Plant Soil* 264(1-2): 159-169.
- Fillery IRP, De Datta SK, Craswell ET (1986). Effect of phenyl phosphorodiamidate on the fate of urea applied to wetland rice fields. *Fert. Res.* 9: 251-263.
- Fillery IRP, Simpson JR, De Datta SK (1984). Influence of field environment and fertilizer management on ammonia loss from flooded rice. *SSSAJ* 48: 914-920.
- Fitzgerald JW, Stickland TC (1987). Mineralization of organic sulphur in the O-horizon of a hardwood forest: involvement of sulphatase enzyme. *Soil Biol. Biochem.* 19: 779-781.
- Fitzgerald JW (1976). Sulphate ester formation and hydrolysis: a potentially important yet often ignored aspect of the sulphur cycle of aerobic soils. *Bacteriol. Rev.* 40: 628-721.
- Frank T, Malkomes HP (1993). Influence of temperature on microbial activities and their reaction to the herbicide Goltix in different soils under laboratory conditions. *Zentralblatt für Mikrobiol.* 148: 403-412.
- Gal SW (1992). Purification and characterization of chitinase isoenzymes and cloning of a gene for 58kD from *Settaria marcescens* KCTC2172. Doctor's thesis, Gyeongsang National University.
- Galstian AS, Awungian ZS (1974). Significance of the enzymes in oxidation of Fe and Mn oxides in soil (in Russian). *Trans. 10th Intern. Congress Soil Sci. III.* ANauka@ Publishing House, Moscow, pp. 130-135.
- Ganeshamurthy AM, Singh G, Singh NT (1995). Sulphur status and response of rice to sulphur on some soils of Andaman and Nicobar Islands. *J. Indian Soc. Soil Sci.* 43: 637-641.
- Garcia C, Hernández T (1997). Biological and biochemical indicators in derelict soils subject to erosion. *Soil Biol. Biochem.* 29: 171-177.
- Geiger G, Federer P, Sticher H (1993). Reclamation of heavy metal-contaminated soils: field studies and germination experiments. *J. Environ. Qual.* 22: 201-207.
- Glinski J, Stepniowski W (1985). *Soil Aeration and its Role for Plants*. CRC Press, Boca Raton, Florida.
- Goldstein AH (1992). Phosphate starvation inducible enzymes and proteins in higher plants. In: Wray JL (ed.) *Society for Experimental Biology Seminar series 49. Inducible plant proteins*. Cambridge University Press, Cambridge, pp. 25-44.
- Gomah AM (1980). CM-Cellulase activity in soil as affected by addition of organic material, temperature, storage and drying and wetting cycles. *Zeitschrift fuer Pflanzenernaehrung und Bodenkunde.* 143: 349-356.
- Gould WD, Cook FD, Webster GR (1973). Factors affecting urea hydrolysis in several Alberta soils. *Plant Soil* 38: 393-401.
- Guan SY (1989). Studies on the factors influencing soil enzyme activities: Effect of organic manures on soil enzyme activities and N and P transformations. *Acta Pedol. Sinica.* 26: 72-78.
- Gunnison D, Engler RM, Patrick WH Jr (1985). Chemistry and microbiology of newly flooded soils: relationship to reservoir - water quality. *Microb. Processes Reservoirs.* 3: 39-57.
- Gupta VVSR, Farrell RE, Germida JJ (1993). Activity of arylsulphatases in Saskatchewan soils. *Can. J. Soil Sci.* 73: 341-347.
- Haanstra L, Doelman P (1991). An ecological dose-response model approach to short- and long-term effects of heavy metals on arylsulphatase activity in soil. *Biol. Fert. Soils.* 11: 18-23.
- Hadar Y, Harman GE, Taylor AG, Norton JA (1983). Effect of pregermination of pea and cucumber seeds and of seed treatment with *Enterobacter cloacae* on rots caused by *Pythium* spp. *Phytopathol.* 73: 1322-1325.
- Hans YW, Snivasan VR (1969). Purification and characterization of β -glucosidases of *Alcaligenes faecalis*. *J. Bacteriol.* 100: 1355-1363.
- Haran S, Logendra S, Saskar M, Bratanova M, Raskin I (2000). Characterization of Arabidopsis acid phosphatase promoter and regulation acid phosphatases expression. *Plant Physiol.* 124: 615-626.
- Hayano K, Katami A (1977). Extraction of β -glucosidase activity from pea field soil. *Soil Biol. Biochem.* 9: 349-351.
- Hayano K, Takeuchi M, Ichishima E (1987). Characterization of a metalloproteinase component extracted from soil. *Biol. Fert. Soils.* 4: 179-183.
- Hayano K, Tubaki K (1985). Origin and properties of β -glucosidase activity of tomato-field soil. *Soil Biol. Biochem.* 17: 553-557.
- Hayes JE, Richardson AE, Simpson RJ (1999). Phytase and acid phosphatases activities in roots of temperate pasture grasses and legumes. *Austr. J. Plant Physiol.* 26: 801-809.
- Hoffmann G (1959). Verteilung und herkunft eigener enzyme in boden. *Z. PflErnähr. Düng. Bodenk.* 85: 97-104.
- Hope CFA, Burns RG (1987). Activity, origins and location of cellulases in a silt loam soil. *Biol. Fert. Soils* 5: 164-170.
- Izaguirre-Mayoral ML, Flores S, Carballo O (2002). Determination of acid phosphatases and dehydrogenase activities in the rhizosphere of nodulated legume species native to two contrasting savannah sites in Venezuela. *Biol. Fert. Soils.* 35: 470-472.
- James ES, Russel LW, Mitrick A. (1991). Phosphate stress response in hydroponically grown maize. *Plant Soil.* 132: 85-90.
- Jordan D, Kremer RJ (1994). Potential use of microbial activity as an indicator of soil quality. In: Pankhurst CE, Double BM, Gupta VVSR, Grace PR (Eds.): *Soil biota. Management in sustainable farming systems*, CSIRO Australia pp. 245-249.
- Juma NG, Tabatabai MA (1977). Effects of trace elements on phosphatase activity in soils. *SSSAJ* 41: 343-346.
- Kai M, Takazumi K, Adachi H, Wasaki J, Shinano T, Osaki M (2002). Cloning and characterization of four phosphate transporter cDNAs in tobacco. *Plant Sci.* 163: 837-846.
- Kandeler E (1996). Nitrate. In: Schinner F, Öhlinger R, Kandeler E, Margesin R (eds). *Methods in soil biology*. Springer, Berlin Heidelberg New York, pp. 408-410.
- Kanfer JN, Mumford RA, Raghavan SS, Byrd J (1974). Purification of β -glucosidase activities from bovine spleen affinity chromatography. *Anal. Biochem.* 60: 200-205.
- Karthikeyan AS, Varadarajan DK, Mukatira UT, D'Urzo MP, Damaz B, Raghobhama KG (2002). Regulated expression of Arabidopsis phosphate transporters, *Plant Physiol.* 130: 221-233.
- Kertesz MA, Mirleau P (2004). The role of soil microbes in plant sulphur nutrition. *J. Exp. Bot.* 55(404): 1939-1945.
- Khaziyev FK, Gulke AY (1991). Enzymatic activity of soils under agrocenoses: status and problems. *Pochvovedenie*, 8: 88-103.
- King NJ (1967). Glucoamylase of *Coniophora cerebella*. *Biochem. J.* 105: 577-583.
- Kiss S, Dragan-Bularda M, Radulescu D (1978). Soil polysaccharidases: activity and agricultural importance. In: *Soil Enzymes* (Burns RG, Ed.), pp. 117-147. Academic Press, London.
- Kissel DE, Cabrera ML, Ferguson RB (1988). Reactions of ammonia and urea hydrolysis products with soil. *SSSAJ* 52: 1793-1796.
- Klein DA (1989). Cellulose functions in arid soil development. *Arid Soil Res. Rehab.* 3: 185-198.
- Klose S, Moore JM, Tabatabai MA (1999). Arylsulphatase activity of microbial biomass in soils as affected by cropping systems. *Biol. Fert. Soils.* 29: 46-54.
- Klose S, Tabatabai MA (1999). Arylsulphatase activity of microbial biomass in soils. *SSSAJ* 63: 569-574.
- Kuperman RG, Carreiro MM (1997). Soil heavy metal concentrations,

- microbial biomass and enzyme activities in a contaminated grassland ecosystem. *Soil Biol. Biochem.* 29: 179-190.
- Ladd JN (1972). Properties of proteolytic enzymes extracted from soil. *Soil Biol. Biochem.* 4: 227-237.
- Ladd JN (1978). Origin and range of enzymes in soil. In: *Soil Enzymes* (Bums RG, Ed.), pp. 51-96. Academic Press, London.
- Ladd JN, Butler JHA (1969a). Inhibitory effect of soil humic compounds on the proteolytic enzyme, Pronase. *Austr. J. Soil Res.* 7: 241-251.
- Ladd JN, Butler JHA (1969b). Inhibition and stimulation of proteolytic enzyme activities by soil humic acids. *Austr. J. Soil Res.* 7: 253-261.
- Ladd JN, Jackson RB (1982). In: Stevenson FJ (Ed.). *Nitrogen in Agricultural Soils*, Am. Soc. Agron., WI. pp. 173-228.
- Leiro's MC, Trasar-Cepeda C, García-Fernández F, Gil-Sotres F (1999). Defining the validity of a biochemical index of soil quality. *Biol. Fert. Soils.* 30: 140-146.
- Li D, Zhu H, Liu K, Liu X, Leggewie G, Udvardi M, Wang D (2002). Purple acid phosphatases of *Arabidopsis thaliana*. *J. Biol. Chem.* 277: 27772-27781.
- Li M, Shinano T, Tadano T (1997). Distribution of exudates of lupin roots in the rhizosphere under phosphorus deficient conditions. *Soil Sci. Plant Nutr.* 43: 237-245.
- Li Y, Guohua M, Fanjun C, Jianhua Z, Fusuo Z (2004). Rhizosphere effect and root growth of two maize (*Zea mays* L.) genotypes with contrasting P efficiency at low P availability. *Plant Sci.* 167: 217-223.
- Lizarazo LM, Jordá JD, Juárez M, Sánchez-Andreu J (2005). Effect of humic amendments on inorganic N, dehydrogenase and alkaline phosphatase activities of a Mediterranean soil. *Biol. Fert. Soils.* 42: 172-177.
- Madejo'n E, Burgos P, López R, Cabrera F (2001). Soil enzymatic response to addition of heavy metals with organic residues. *Biol. Fert. Soils* 34: 144-150.
- Martinez CE, Tabatabai MA (1997). Decomposition of biotechnology by-products in soils. *J. Environ. Qual.* 26: 625-632.
- Mayaudon J, Batistic L, Sarkar JM (1975). Propriétés des activités protéolytiques extraites des sols frais. *Soil Biol. Biochem.* 7: 281-286.
- McCarthy GW, Siddaramappa R, Reight RJ, Coddling EE, Gao G (1994). Evaluation of coal combustion by products as soil liming materials: their influence on soil pH and enzyme activities. *Biol. Fert. Soils.* 17: 167-172.
- McGill WB, Colle CV (1981). Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma.* 26: 267-286.
- McLaren AD (1975). Soil as a system of humus and clay immobilised enzymes. *Chem. Scripta.* 8: 97-99.
- Melouk HA and Horner CE (1973). β -glucosidase from *Phoma strasseri* and its possible role in a disease of peppermint. *Phytopathology*, 63: 973-975.
- Mikkelsen DS, De Datta SK, Obcemea WN (1978). Ammonia volatilization losses from flooded rice soils. *SSSAJ* 49: 725-730.
- Miller SS, Liu J, Allan DL, Menzhuber CJ, Fedorova M, Vance CP (2001). Molecular control of acid phosphatase secretion into the rhizosphere of proteoid roots from phosphorous stressed white lupin. *Plant Physiol.* 127: 594-606.
- Miwa T, Ceng CT, Fujisaki M and Toishi A (1937). Zur Frage der Spezifität der Glykosidasen. I. Verhalten von β -d-glucosidasen verschiedener Herkunft gegenüber den β -d-Glucosiden mit verschiedenen Aglykonen. *Acta Phytochim.* (Tokyo). 10: 155-170.
- Mobley HLT, Hausinger RP (1989). Microbial urease: significance, regulation and molecular characterization. *Microbiol. Rev.*, 53: 85-108.
- Muchhal US, Pardo JM, Raghothama KG (1996). Phosphate transporters from the higher plant *Arabidopsis*. *Proc. Natl. Acad. Sci. USA.* 93: 10519-10523.
- Mudge SR, Rae AL, Diatloff E, Smith FW (2002). Expression analysis suggests novel roles for members of Pht1 family of phosphate transporters in *Arabidopsis*. *Plant J.* 31: 341-353.
- Mulvaney RL, Bremner JM (1981). Control of urea transformation in soils. In *Soil Biochemistry*, Vol. 5 (Paul EA, Ladd JN Eds) pp. 153-196. Marcel Dekker, New York.
- Mungai WN, Motavalli PP, Kremer RJ, Nelson KA (2005). Spatial variation in soil enzyme activities and microbial functional diversity in temperate alley cropping systems. *Biol. Fert. Soils* 42: 129-136.
- Myers MG, McGarity JW (1968). The urease activity in profiles of five great soil groups from northern New South Wales. *Plant Soil.* 28(1): 25-37.
- Nakas JP, Gould WD, Klein DA (1987). Origin and expression of phosphatase activity in a semi-arid grassland soil. *Soil Biol. Biochem.* 19: 13-18.
- Nannipieri P, Ceccanti B, Bianchi D, Bonmati M (1985). Fractionation of hydrolase-humus complexes by gel chromatography. *Biol. Fert. Soils* 1: 25-29.
- Nannipieri P, Ceccanti B, Cervelli S and Sequi P (1978). Stability and kinetic properties of humus-urease complexes. *Soil Biol. Biochem.* 10: 143-147.
- Nannipieri P, Ceccanti B, Cervelli S, Matarese E (1980). Extraction of phosphatase, urease, proteases, organic carbon, and nitrogen from soil. *SSSAJ* 44: 1011-1016.
- Nannipieri P, Ceccanti B, Conti C, Bianchi D (1982). Hydrolases extracted from soil: their properties and activities. *Soil Biol. Biochem.* 14: 257-263.
- Nannipieri P, Sequi P, Fusi P (1996). Humus and enzyme activity. In: Piccolo A (Ed.), *Humic Substances in Terrestrial Ecosystems*. Elsevier, New York, pp. 293-328.
- Ndakidemi PA (2006). Manipulating legume/cereal mixtures to optimize the above and below ground interactions in the traditional African cropping systems. *Afr. J. Biotechnol.* 5 (25): 2526-2533.
- Ndiaye EL, Sandeno JM, McGrath D, Dick RP (2000). Integrative biological indicators for detecting change in soil quality. *Am. J. Altern. Agric.* 15: 26-36.
- Okazaki M, Hirata E, Tensho K (1983). TTC reduction in submerged soils. *Soil Sci. Plant Nutr.* 29: 489-497.
- Ordentlich A, Elad Y, Chet I (1988). The role of chitinase of *Serratia marcescens* in biocontrol of *Sclerotium rolfsii*. *Phytopathology*, 78: 84-88.
- Pancholy SK, Rice EL (1973). Soil enzymes in relation to old field succession; amylase, cellulose, invertase, dehydrogenase and urease. *SSSAJ* 37: 47-50.
- Park D (1960). Antagonism—the background of soil fungi. In: Parkinson D, Waid JS (Eds.). *The Ecology of Soil Fungi*, Liverpool University Press, Liverpool, pp. 148-159.
- Patra DD, Brookes PC, Coleman K, Jenkinson DS (1990). Seasonal changes of soil microbial biomass in an arable and a grassland soil which have been under uniform management for many years. *Soil Biol. Biochem.* 22: 739-742.
- Patrick ZA (1955). The peach replant problem in Ontario. II. Toxic substances from microbial decomposition products of peach root residues. *Can. J. Bot.* 33: 461-486.
- Pazur JH (1965). Enzymes in the synthesis and hydrolysis of starch. In: *Starch: Chemistry and Technology*. Vol. 1 Fundamental aspects (Whistler R, Paschall EF Eds.) pp. 133-175. Academic press, New York.
- Pedrazzini FR, McKee KL (1984). Effect of flooding on activities of dehydrogenase in rice (*Oryza sativa* L.) roots. *Soil Sci. Plant Nutr.* 30: 359-366.
- Perucci P, Scarponi L, Businelli M (1984). Enzyme activities in a clay-loam soil amended with various crop residues. *Plant Soil.* 81: 345-351.
- Petker AS, Rai PK (1992). Effect of fungicides on activity, secretion of some extra cellular enzymes and growth of *Alternaria alternata*. *Indian J. Appl. Pure. Biol.* 7(1): 57-59.
- Pettit NM, Smith ARJ, Freedman RB, Burns RG (1976). Soil urease: activity, stability and kinetic properties. *Soil Biol. Biochem.* 8: 479-484.
- Pitchel JR, Hayes JM (1990). Influence of fly ash on soil microbial activity and populations. *J. Environ. Qual.* 19: 593-597.
- Polacco JC (1977). Is nickel a universal component of plant ureases? *Plant Sci. Lett.* 10: 249-255.
- Rad JC, Navarro-González M, González-Carcedo S (1995). Characterization of proteases extracted from a compost of municipal solid wastes. *Geomicrobiol. J.* 13: 45-56.
- Reddy GB and Faza A (1989). Dehydrogenase activity in sludge amended soil. *Soil Biol. Biochem.* 21(2): 327.
- Rees ET, Siu RGH, Levinson HS (1950). The biological degradation of soluble cellulose derivatives and its relationship to the mechanisms of cellulose hydrolysis. *J. Bacteriol.* 59: 485-497.

- Reese ET (1975). Polysaccharides and the hydrolysis of insoluble substrates. In: *Biological Transformation of Wood by Microorganisms* (Leise W. Ed.), pp. 165-181. Springer-Verlag, New York.
- Richmond PA (1991). Occurrence and functions of native cellulose. In: *Biosynthesis and Biodegradation of Cellulose* (Haigler CH and Weimer PJ Eds), pp. 5-23. Dekker, New York.
- Ross DJ (1968). Activities of enzymes hydrolysing sucrose and starch in some grassland soils. *Trans. 9th Int. Congr. Soil Sci.* 3: 299-308.
- Ross DJ (1975a). Studies on a climosequence of soils in tussock grasslands-5. Invertase and amylase activities of topsoils and their relationships with other properties. *NZ J. Sci.* 18: 511-518.
- Ross DJ (1976). Invertase and amylase activities in ryegrass and white clover plants and their relationships with activities in soils under pasture. *Soil Biol. Biochem.* 8: 351-356.
- Ross DJ, Roberts HS (1968). A study of activities of enzymes hydrolysing sucrose and starch and of oxygen uptake in a sequence of soils under tussock grassland. *J. Soil Sci.* 19: 186-196.
- Ross DJ, Roberts HS (1970). Enzyme activities and oxygen uptakes of soils under pasture in temperature and rainfall sequences. *J. Soil Sci.* 21: 368-381.
- Rotini OT (1935). La trasformazione enzimatica dell'urea nel terreno. *Ann. Labor. Ric. Ferm. Spallanzani.* 3: 143-154.
- Rubidge T (1977). The effect of moisture content and incubation temperature upon the potential cellulase activity of John Innes no. 1 soil (ISSN. 0020-6164). *Int. Biodeterior. Bul.* 13: 39-44.
- Sarathchandra SU, Perrott KW (1981). Determination of phosphatase and arylsulphatase activity in soils. *Soil Biol. Biochem.* 13: 543-545.
- Schmidt G, Laskowski Sr M (1961). Phosphate ester cleavage (Survey). In: Boyer PD, Lardy H, Myrback K (eds). *The enzymes*, 2nd edn. Academic Press, New York, pp. 3-35.
- Shapira R, Ordentlich A, Chet I, Oppenheim AB. (1989). Control of plant diseases by chitinase expressed from cloned DNA in *Escherichia coli*. *Phytopathology*, 79: 1246-1249.
- Shawale JG, Sadana J (1981). Purification, characterization and properties of β -glucosidase enzyme from *Sclerotium rolfsii*. *Archives Biochem. Biophys.* 207: 185-196.
- Sherrod LL, Domsch KH (1970). Amino acids in exudates of healthy and fungus-affected pea roots. *Arch. Mikrobiol.* 70(3): 240-242.
- Simpson JR, Freney JR (1988). Interacting processes in gaseous nitrogen loss from urea applied to flooded rice fields. In: *Proceedings of International Symposium on Urea Technology and Utilization* (Pushparajah E, Husin A, and Bachik AT, Eds), pp. 281-290. Malaysian Society of Soil Science, Kuala Lumpur.
- Simpson JR, Freney JR, Muirhead WA, Leuning R (1985). Effects of phenylphosphorodiamidate and dicyandiamide on nitrogen loss from flooded rice. *SSSAJ* 49: 1426-1431.
- Simpson JR, Freney JR, Wetselaar R, Muirhead WA, Leuning R and Denmead OT (1984). Transformations and losses of urea nitrogen after application to flooded rice. *Austr. J. Agric. Res.* 35: 189-200.
- Singh PP, Shin YC, Park CS, Chung YR (1999). Biological control of *Fusarium wilt* of cucumber by chitinolytic bacteria. *Phytopathology*, 89: 92-99.
- Sinsabaugh RL, Antibus RK, Linkins AE (1991). An enzymic approach to the analysis of microbial activity during plant litter decomposition. *Agric. Ecosyst. Environ.* 34: 43-54.
- Sinsabaugh RL, Antibus RK, Linkins AE, McClaugherty CA, Rayburn L, Repert D, Weiland T (1993). Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecol.* 74: 1586-1593.
- Sinsabaugh RL, Linkins AE (1989). Natural disturbance and the activity of *Trichoderma viride* cellulase complex. *Soil Biol. Biochem.* 21: 835-839.
- Skujins J (1967). Enzymes in soil. In: *Soil Biochemistry* (McLaren D and Peterson GH (Eds.) pp. 371-414. Marcel Dekker, New York.
- Skujins J (1973). Dehydrogenase: An indicator of biological activities in arid soils. *Bull. Ecol. Res. Comm. (Stockholm)*. 17: 235-241.
- Skujins J (1976). Enzymes in soil. In: McLaren AD, Peterson GH (eds). *Soil Biochem.*, vol 1. Dekker, New York, pp. 371-414.
- Skujins J (1976). Extracellular Enzymes in Soil. *CRC Crit. Rev. Microbiol.* 4: 383-421.
- Skujins J (1978). Soil enzymology and fertility index—a fallacy? History of abiotic soil enzyme research. In: Burns RG (Ed.), *Soil Enzymes*. Academic Press, London, pp. 1-49.
- Sneh B (1981). Use of rhizosphere chitinolytic bacteria for biological control of *Fusarium oxysporum* f. sp. *dianthi* incantation. *Phytopathologisches Zeitschrift* 100: 251-256.
- Speir TW, Ross DJ (1978). Soil phosphatase and sulphatase. In: Burns RG (Ed.). *Soil Enzymes*, pp. 197-250, Academic Press, London, UK, p. 380.
- Spencer B (1958). Studies on sulphatases: 20. Enzymic cleavage of aryl hydrogen sulphates in the presence of H, O, *Biochem. J.* 69: 155-159.
- Spier TW, Lee R, Eisebeth AP, Cairns A (1980). A comparison of sulphatase, urease and phosphatase activity in planted and fallow soils. *Soil Biol. Biochem.* 12: 281-291.
- Srinivasulu M, Rangaswamy V (2006). Activities of invertase and cellulase as influenced by the application of tridemorph and captan to groundnut (*Arachis hypogaea*) soil. *Afr. J. Biotechnol.* 5(2): 175-180.
- Staddon WJ, Duchesne LC, Trevors JT (1998). Impact of clear-cutting and prescribed burning on microbial diversity and community structure in a Jack pine (*Pinus banksiana* Lamb.) clear-cut using BIOLOG gram-negative microplates. *World J. Microbiol. Technol.* 14: 119-123.
- Stangel PJ (1984). World nitrogen situation-trends, out-look, and requirements. In: *Nitrogen in Crop Production* (Hauck RD Ed.), pp.23-53. American Society of Agronomy, Madison, Wisc.
- Strickland TC, Fitzgerald JW (1984). Formation and mineralization of organic sulphur in forest soils. *Biogeochemistry*, 1: 79-95.
- Tabatabai MA (1977). Effect of trace elements on urease activity in soils. *Soil Biol. Biochem.* 9: 9-13.
- Tabatabai MA (1982). Soil enzyme. In: *Methods of Soil Analysis, Part 2* (Page AL Ed.), Am. Soc. Agron. Madison, Wisc. pp. 903-948.
- Tabatabai MA (1982). Sulphur. In: *Methods of Soil Analysis. Part II. Chemical and microbiological Properties* (Page AL, Miller RH and Keeney DR. Eds). Soil Sci. Soc. Am., Madison, pp. 501-538.
- Tabatabai MA (1994). Soil enzymes. In: Weaver RW, Angle JS, Bottomley PS (eds) *Methods of soil analysis, part 2. Microbiological and biochemical properties*. SSSA Book Series No. 5. Soil Sci. Soc. Am. Madison, Wis., pp. 775-833.
- Tabatabai MA, Bremner JM (1970a). Arylsulphatase activity of soils. *SSSAP* 34: 225-229.
- Tabatabai MA, Bremner JM (1970b). Factors affecting soil arylsulphatase activity. *SSSAP* 34: 427-429.
- Tabatabai MA, Bremner JM (1971). Michaelis constants of soil enzymes. *Soil Biol. Biochem.* 3: 317-323.
- Tarafdar JC, Jungk A (1987). Phosphatase activity in the rhizosphere and its relation to the depletion of soil organic phosphorus. *Biol. Fert. Soils.* 3(4): 199-204.
- Thoma JA, Spradlin JE, Dygert S (1971). Plant and animal amylases. In: *The Enzymes* (Boyer PD Ed.) 5: 115-189.
- Tiwari MB, Tiwari BK, Mishra RR (1989). Enzyme activity and carbon dioxide evolution from upland and wetland rice soil under three agricultural practices in hilly regions. *Biol. Fert. Soils* 7: 359-364.
- Tomar JS, MacKenzie AF (1984). Effects of catechol and *p*-benzoquinone on the hydrolysis of urea and energy barriers of urease activity in soil. *Can. J. Soil Sci.* 64: 51-60.
- Trevors JT (1984). Dehydrogenase activity in soil: A comparison between the INT and TTC assay. *Soil Biol. Biochem.* 16: 673-674.
- Tweddel RJ, Jabaji-Hare SH, Charest PM (1994). Production of chitinase and β -1,3-glucanase by *Stachybotrys elegans*, a mycoparasite of *Rhizoctonia solani*. *Appl. Environ. Microbiol.* 60: 489-495.
- Tyler G (1981). Heavy metals in soil biology and biochemistry. In: *Soil Biochem.* Vol. 5 (Paul EA, Ladd JN Eds), pp. 371-414. Dekker, New York.
- Van Gleemput O, Wang Z (1991). Urea transformations and urease inhibitors. *Tr. Soil Sci.* 1: 45-51.
- Versaw WK, Harrison MJ (2002). A Chloroplast Phosphate Transporter, PHT2; 1, Influences Allocation of Phosphate within the Plant and Phosphate-Starvation Responses. *Plant Cell* 14: 1751-1766.
- Vincent PG, Sislter HD (1968). Mechanisms of antifungal action of 2, 4, 5, 6-tetrachloroisophthalonitrile. *Physiol. Plant* 21: 1249-1264.
- Vlek PLG, Byrnes BH (1986). The efficacy and loss of fertilizer N in lowland rice. *Fert. Res.* 9: 131-147.

- Vong PC, Dedourge O, Lasserre-Joulin F, Guckert A (2003). Immobilized-S, microbial biomass-S and soil arylsulphatase activity in the rhizosphere soil of rape and barley as affected by labile substrate C and N additions. *Soil Biol. Biochem.* 35: 1651-1661.
- Watson AP, van Hook RI, Jackson DR, Reichle DE (1976). Impact of lead mining and smelting complex on the forest floor litter arthropod fauna in the New Lead Belt Region of Southern Missouri. ORNL/NSF/EATC-30, Oak Ridge National Laboratory.
- Wenzel WW, Pollak MA, Riedler C, Zischka RR, Blum WEH (1995). Influence of site conditions and heavy metals on enzyme activities of forest topsoil. In: *Environmental Impact of Soil Component Interactions-Metals, Other Inorganics, and Microbial Activities*, (Huang PM, Berthelin J, Bollag JM, McGill WN, Page AL, Eds.) pp. 211-225, CRC, Baton Rouge.
- White AR (1982). Visualization of cellulases and cellulose degradation. In: *Cellulose and Other Natural Polymer Systems: Biogenesis, Structure, and Degradation* (Brown RM Jr, Ed.), pp. 489-509. Plenum Press, New York.
- Wick B, Kühne RF, Vlek PLG (1998). Soil microbiological parameters as indicators of soil quality under improved fallow management systems in southwestern Nigeria. *Plant Soil* 202: 97-107.
- Wilke BM (1991). Effect of single and successive additions of cadmium, nickel and zinc on carbon dioxide evolution and dehydrogenase activity in a sandy Luvisol. *Biol. Fert. Soils* 11: 34-37.
- Williams CH (1975). The chemical nature of sulphur compounds in soil. In: *Sulphur in Australasian Agriculture* (McLachlan KD Ed.), pp. 21-30. Sydney University Press.
- Wirth SJ, Wolf GA (1992). Micro-plate colourimetric assay for endo-acting cellulose, xylanase, chitinase, 1,3- β -glucosidase and amylase extracted from forest soil horizons. *Soil Biol. Biochem.* 24(6): 511-519.
- Wood TM (1991). Fungal cellulases. In: *Biosynthesis and Biodegradation of Cellulose* (Haigler CH, Weimer PJ. Eds), pp. 491-533. Marcel Dekker, New York.
- Wright AL, Reddy KR (2001). Phosphorus Loading Effects on Extracellular Enzyme Activity in Everglades Wetland Soil. *SSSAJ* 65: 588-595.
- Yadav RS, Tarafdar JC (2001). Influence of organic and inorganic phosphorous supply on the maximum secretion of acid phosphatase by plants. *Biol. Fert. Soils* 34: 140-143.
- Yang Z, Liu S, Zheng D, Feng S (2006). Effects of cadmium, zinc and lead on soil enzyme activities. *J. Environ. Sci.* 18(6): 1135-1141.
- Zantua MI, Bremner JM (1977). Stability of urease in soils. *Soil Biol. Biochem.* 9: 135-140.