Microbial Enzymes: Role in Soil Fertility

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Abstract Chemical, biochemical, and physicochemical reactions are all involved in nutrient cycling in soil. Enzymes catalyze all biochemical processes in soil. Soil enzymes catalyze several biochemical processes that ensure the transformation of organic materials and the release of inorganic nutrients for plant growth and nutrient cycling. As a result of the significant role played by soil enzymes in improving the fertility of soil, an in-depth evaluation of the influence of soil microbial enzymes on the fertility of soil is essential for effective maintenance of soil fertility, utilization of soil resources, and enhancement of plant productivity. This chapter discusses (1) the detailed role of soil microbial enzymes in improving the fertility of soil, (2) the mechanisms of action of soil enzymes, and (3) the factors influencing the enzyme activity in soil.

1 Introduction

Soil is a nonrenewable, dynamic resource. It is an essential component of a terrestrial ecosystem, providing basic support to all living organisms on the planet. In various land-use scenarios, soil fertility is an important indicator of good agricultural productivity (Almeida, Naves, & Mota, 2015). The fertility of soil is referred to as its capability to function continuously within land-use boundaries and ecosystems, as a vital living system for biological productivity and animal, plant, and human well-being (Doran & Parkin, 1994). The status of soil has an impact on the ecosystem, food production, and global ecological equilibrium (Adetunji, Lewu, Mulidzi, & Ncube, 2017; Binkley & Fisher, 2012). Soil fertility is closely linked to biological properties that are extremely sensitive to changes in the environment. The soil microbiota and enzymes are closely related and play important roles in improving the fertility of soil (Joshi, Mohapatra, & Mishra, 2018; Pajares, Gallardo, & Masciandaro, 2011). Therefore, the sustainability of the soil ecosystem can be assessed using biologically based indicators (Adetunji et al., 2017; Piotrowska-Dlugosz & Charzynski, 2015). Recently, the biodegradability capacity of microorganisms has been assessed through the evaluation of the activity of soil enzymes (Fioretto, Papa, Curcio, Sorrentino, & Fuggi, 2000). The different microbes in soil establish a relationship with the other biological systems and release enzymes. In the soil environment, microorganisms release enzymes that break down organic substances into simple soluble molecules (Almeida et al., 2015). In soil, there are two types of enzymes. Constitutive enzymes are those that are always present in the body in a consistent amount for metabolic action. The addition of any substrate has no effect on these enzymes (Das & Varma, 2011). Phosphofructokinase, pyruvate kinase, hexokinase, phosphoglucose isomerase, and other enzymes involved in the glycolytic pathway, for example, are constitutive enzymes (Maitra & Lobo, 1971). Other enzymes in the soil such as urease and phosphatase are also constitutive enzymes (Kumar & Sharma, 2019; Margalef et al., 2017). Inducible or inductive enzymes are found in limited amounts and sometimes may be absent. The concentration of such enzymes may vary and increase with the presence of a substrate. For

instance, cellulase (Kandeler, 2015) and amidase (Das & Varma, 2011) are some of the inductive enzymes found in soil.

Soil enzymes that are synthesized by soil-inhabiting microbes perform important functions in the cycling of nutrients and indicate soil fertility and microbial activity (Joshi et al., 2018). Extracellular and intracellular soil enzymes such as glucosidase (Almeida et al., 2015) and hydrolase (Bautista-Cruz & Ortiz-Hernandez, 2015) catalyze the breakdown of organic materials, whereas urease, amidase, and arylsulfatase are concerned with nutrient mineralization (Das & Varma, 2011; Kumar & Sharma, 2019). The decomposition of heavy metals in soil is also aided by catalase enzymes such as phosphatase and dehydrogenase. These are crucial in the remediation of heavy metal-impacted soils (Khan, Cao, Hesham, Xia, 2007). Soil enzymes catalyze and promote a variety of biochemical processes that result in soil organic matter transformation, breakdown of organic residues, mineralization of accessible nutrients for plant growth, and soil aggregation (Balezentiene, 2012). Enzymes are thus linked to the rate of breakdown. Enzymes are active facilitators of the degradation processes of soil mineral organic components. For instance, urease participates in nitrogen cycling and hydrolysis of urea to NH_3 and CO_2; sucrase catalyzes the hydrolysis of sucrose to release monosaccharides and improve the soil-soluble nutrients; and phosphatase hydrolyzes phosphate ester and participates in cycling and mineralization of phosphorus (Adamczyk, Kilpeläinen, Kitunen, & Smolander, 2014; Zhang et al., 2018). Earlier studies have revealed that the enzymes associated with the mineralization of N, C, and P are closely related to N: C: P stoichiometry of soil (Stock, Kster, Dippold, Nájera, & Kuzyakov, 2019; Xu et al., 2017). Thus, enzyme activity objectively reflects the fertility of soil. A decline in the activity of soil enzymes indicates a decrease in the quality of soil (Zhu, Wang, Chen, Li, & Wu, 2019). Therefore, these catalytic activities provide some vital information for the assessment of the rates of important reactions. Soil microbial enzyme activities (1) are largely connected to soil physical attributes, microbial biomass, and organic matter and (2) change more readily than do the other indicators, signaling changes in soil quality or health faster (Dick, 1994). The activity of soil enzymes can be used to assess soil productivity, microbial activity, and the inhibitory effects of soil pollutants. In comparison to other properties, the activity of soil enzymes responds quickly to management strategies such as crop rotations, amendments, and tillage systems (Lehman et al., 2015). Moreover, the responses of enzyme activity correlate with the other soil properties, which suggest that they can be utilized to differentiate how management practices may influence soil parameters such as pH, organic materials, and distribution of nutrients (Acosta-Martinez, Cano, & Johnson, 2018; Lehman et al., 2015). Therefore, an in-depth evaluation of the influence of soil microbial enzymes on the fertility of soil is essential for the effective maintenance of soil fertility, utilization of soil resources, and enhancement of plant productivity. This chapter discusses (1) the detailed role of soil microbial enzymes in improving the fertility of soil, (2) the mechanisms of action of soil enzymes, and (3) the factors influencing the enzyme activity in soil.

2 The Role of Microbial Enzymes in Improving Soil Fertility

Soil can be viewed as a biological entity. In other words, it is a living system where biochemical reactions take place, and those reactions are catalyzed by enzymes. It is believed that, without enzymes, the soil will be a lifeless and unaltered entity (Alkorta et al., 2003). Microbially aided reactions, which are catalyzed by enzymes, are the backbone of the performance of soil. Such performance includes the cycling of sulfur, phosphorus, nitrogen, and carbon in the soil. In addition, the processes also contribute to the cleanup of contaminated soil through degradation of contaminants such as hydrocarbons or immobilization, e.g., in the case of heavy metals. Enzymatic actions are also involved in the formation of soil structure (Nannipieri, Kandeler, & Ruggiero, 2002). All biochemical processes in soil are aided by enzymes; this makes enzymes suitable indicators of soil biological activity and health (Alkorta et al., 2003). Enzyme activities in soil have been regarded as important parameters that are utilized to biologically assess the function of soil (Alrumman, Standing, & Paton, 2015). Recently, a research has revealed the utilization of enzyme activities in soil as a measure of nutrient and carbon deficiencies, which can be employed to reveal the influence of regional anthropogenic stressors in soil (Pandey & Yadav, 2017).

Microbial enzymes that catalyze the numerous reactions in soil are necessary for the cycling of nutrients, decomposition of organic substances, formation of organic matter, life processes of soil microbes, and stabilization of soil structure (Burns et al., 2013). Some of the enzymes that catalyze the numerous reactions (N, S, C, and P cycling) in soil include ureases, dehydrogenases, phosphatases, catalases, cellulases, proteases, lipases, fluorescein diacetate, arylsulfatases, esterases, hydrolases, etc. (Fig. 1) (Banashree, Smrita, Nath, & Nirmali, 2017). The contributions of these enzymes to soil fertility and health are described in detail.

2.1 Glucosidases

Glucosidases are a group of hydrolytic enzymes that catalyze the breakdown of glycosides. They are extremely diverse, which is the result of the vast variety of glycosidic linkages and variations in substrates (Almeida et al., 2015). The four primary members of the glucosidases family are β- and α-galactosidase and β- and α-glucosidase. In soil, these enzymes are widely spread. The hydrolysis of α-D-glucopyranosides is catalyzed by α-glucosidase, whereas cellobiose and maltose are hydrolyzed by β-glucosidase (Utobo & Tewari, 2015). Glucosidase activity has been found in a variety of microorganisms, including *Flavobacterium johnsoniae* (Okamota, Nakano, Yatake, Kiso, & Kitahata, 2000), *Ceriporiopsis subvermispora* (Magalhaes, Ferraz, & Milagres, 2006), *Penicillium purpurogenum* (Dhake & Patil, 2005), *Lactobacillus plantarum* (Spano, Rinaldi, Ugliano, Beneduce, & Massa, 2005), and *Trichoderma harzianum* (An, Im, Yang, Yang, & Lee, 2005). In soil,

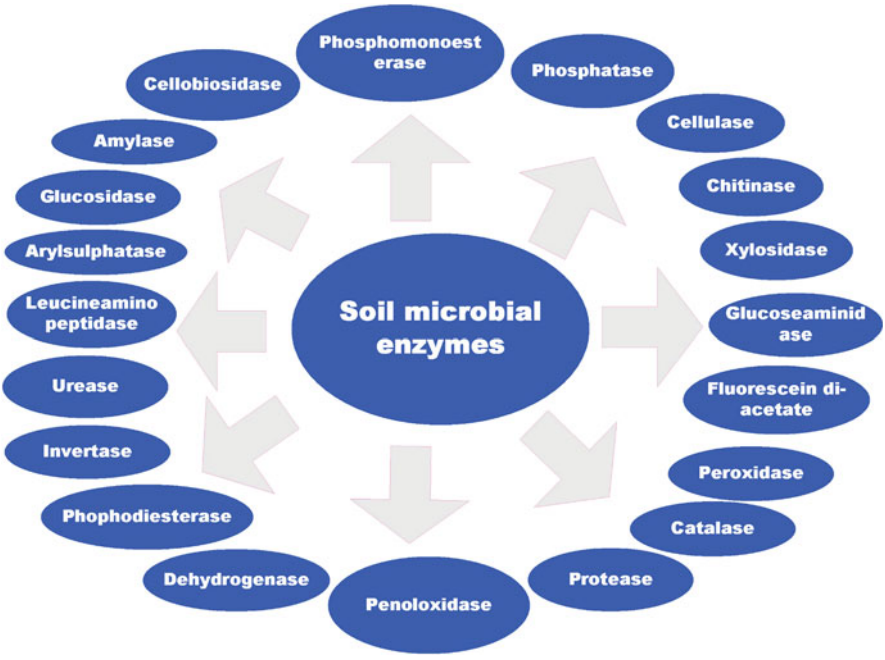

Fig. 1 Soil microbial enzymes

β-glucosidase plays a crucial role by facilitating the breakdown of different β-glucosides found in degrading plant materials (Veena, Poornima, Parvatham, & Sivapriyadharsini, 2011). Many soil bacteria use the end product of the breakdown (glucose) as a source of C for sustenance (Esen, 1993). β-Glucosidase is a crucial measure of soil health because it can stabilize organic materials in soils, represent historical biological activity in soils, and disclose the impacts of management activities on soils (Ndiaye, Sandeno, McGrath, & Dick, 2000). For this, it has been adopted for testing the quality of soil (Bandick & Dick, 1999). β-Glucosidase is highly sensitive to soil management practices and changes in pH (Madejon, Burgos, Lopez, & Cabrera, 2001). Such characteristics make it a useful indicator for assessing the ecological changes that result from the acidification of soil in situations that involve the activities of this enzyme (Das & Varma, 2010). Generally, the activity of β-glucosidase is closely associated with C cycling, organic matter, and biological activity and can provide an early signal of the alterations in organic carbon faster than can be determined using other methods. This forms the basis for its efficient applicability in agricultural practices (Adetunji et al., 2017).

2.2 Cellulases

Cellulose is the most common organic component in soil, accounting for over half of all synthesized biomass. Microbial development and survival are critical in the majority of agricultural soils, and they rely on cellulose as a carbon source in the soil, which serves as the microbe's primary source of energy. However, the enzyme cellulase must degrade cellulose into cellobiose, glucose, and high-molecular-weight oligosaccharides before the carbon can be made available to microorganisms. The breakdown of cellulose and polysaccharides is catalyzed by cellulases (Deng & Tabatabai, 1994). These enzymes are synthesized by a number of microorganisms including bacteria (*Cellulomonas*, *Clostridium*, *Bacillus*, *Trichoderma*, and *Thermomonospora*) and fungi such as *Aspergillus* (Kuhad, Gupta, & Singh, 2011; Micuți, Bădulescu, & Israel-Roming, 2017). The activities of three important enzymes, namely, β-glucosidase, endoglucanase, and cellobiohydrolase, control the cellulose disintegration into glucose. Soil moisture, pH, oxygen content, the quantity of organic matter and/or plant debris, minerals and/or trace elements, organic matter chemical structure, and its position in the soil profile are all factors that influence these enzymes' activities (Arinze & Yubedee, 2000). Considering the sensitiveness of these enzymes toward these factors, their activities can be utilized as an early indication of the status of some physicochemical soil components, hence simplifying soil management in agriculture (Das & Varma, 2010).

2.3 Amylases

Amylase is a starch hydrolyzing enzyme and consists of α- and β-amylase. The enzyme is found abundantly in soil and is essential for the breakdown of starch, which is an important source of carbon for many soil-dwelling beneficial species. α-Amylase breaks down substrates that resemble starch into glucose and/or oligosaccharides, whereas β-amylase breaks down starch to maltose (Thoma, Spradlin, & Dygert, 1971). Amylase is synthesized by bacteria such as *Bacillus amyloliquefaciens*, *Bacillus stearothermophilus*, and *Bacillus licheniformis* and fungal species like *Penicillium expansum*, *Thermomyces lanuginose*, *Aspergillus niger*, and *Aspergillus oryzae* (Micuți et al., 2017; Padma & Pallavi, 2016).

2.4 Phosphatases

Phosphatases belong to a group of enzymes that catalyze the hydrolysis of phosphoric acid anhydrides and esters (Condron, Turner, Cade-Menun, Sims, & Sharpley, 2005). Phosphatase enzymes are also produced by microbes in the soil. The phosphatase phosphomonoesterase is the most studied of the phosphatases

found in soil. Phosphomonoesterase is a hydrolase enzyme that catalyzes the hydrolysis of phosphate monoester into free phosphate for biological absorption (Makoi & Ndakidemi, 2008). Polyphosphates, sugar phosphates, and nucleotides are among the low-molecular P-containing substances hydrolyzed by the enzyme (Dodor & Tabatabai, 2003). Phosphomonoesterase is active under alkaline and acidic conditions depending on its optimum pH. Alkaline phosphatase is active in the alkaline soil of pH 9–11, whereas acid phosphatase dominates in acidic soils with the pH range of 4–6 (Adetunji et al., 2017). The availability and content of phosphatase in soil vary depending on the extent of organic and mineral fertilizers, organic materials, microbial count, and agricultural practices (Banerjee, Sanyal, & Sen, 2012). These enzymes are believed to be important in the cycling of P in the soil environment. Phosphatases have been found to have a substantial relationship with plant development and P stress. Because plants only use inorganic P and a considerable amount of soil P is bonded to organic substances, the mineralization of this organically bound P will be critical because it will provide a valuable source of nutrients to the plants (Nannipieri, Giagnoni, & Landi, 2011). When there is a P shortfall in the soil, the soil microorganisms increase the production of this enzyme dramatically to improve the solubilization and remobilization of P. This has an impact on plants' ability to grow in P-stressed environments (Karthikeyan et al., 2002). As a result, the synthesis and activity of the phosphatase enzyme are directly linked to the requirement for P by microorganisms and plants (Condron et al., 2005). As a result, phosphatase activity can be used to determine the availability of inorganic P for microbes and plants (Piotrowska-Dlugosz & Charzynski, 2015).

2.5 Dehydrogenases

Dehydrogenase enzymes occur as an integral part of microbial cells. They are synthesized by bacteria such as *Pseudomonas entomophila*. The enzymes oxidize the soil organic matter through the transfer of electrons and protons from substrates to recipients. This activity forms part of the respiratory processes of soil microbes and is associated with the soil type and soil water–air conditions (Kandeler, 1996). The activity of dehydrogenase is mostly used to indicate the biological activity in soil. The fact is that the activity of dehydrogenase is part of the respiratory pathways of soil microbes; therefore, knowledge on the activity of dehydrogenase is highly essential as it will provide information on the soil potentials to support the biochemical processes that maintain the fertility of the soil. According to Brzezinska, Stepniewska, and Stepniewski (1998), temperature and the amount of water in soil affect dehydrogenase activity indirectly by changing the redox potentials of the soil. For example, during flooding, the available oxygen is quickly depleted, resulting in a shift in activity from aerobic to anaerobic. In the absence of oxygen, facultative anaerobic bacteria, for example, commence the metabolic processes employing dehydrogenase activity and Fe (III) as a terminal electron acceptor (Galstian & Awungian, 1974). This process may tamper with the availability of Fe to plants.

This type of redox transformation is closely related to microbial respiratory activities in soil. Therefore, the enzyme may serve as a measure of the microbial oxidative activities in soil. Dehydrogenases are often employed to gauge disruptions associated with trace metals, pesticides in soil, and in soil management practices (Frank & Malkomes, 1993; Hassan, Agamuthu, & Fauziah, 2020, 2021). They are also used to determine the type, extent, and significance of contamination in soil (Hassan et al., 2021). For instance, it has been reported that significant activity of dehydrogenase has been recorded in soil contaminated with effluents from the paper and pulp-making industry (McCarthy, Siddaramappa, Reight, Coddling, & Gao, 1994); meanwhile, in soil contaminated with fly ash, the activity was low (Pitchel & Hayes, 1990).

2.6 Peroxidases

Peroxidases are important in the breakdown of lignin, which is an essential component of the plant cell wall. The fact is that lignin constitutes a significant portion of the available polymers on Earth; therefore, its breakdown results in significant contribution to soil N and C pools and makes available nutrients to the soil microbes (Sinsabaugh, 2010). Peroxidase performs an important function in the decontamination of soil polluted with phenolics and toxic metals. It also helps lessen the negative impacts of reactive oxygen species in soil. Peroxidases are synthesized by the Ascomycota and Basidiomycota divisions of fungi as well as by various bacterial species (Micuți et al., 2017; Sinsabaugh, Zak, Gallo, Lauber, & Amonette, 2004).

2.7 Chitinases

Chitinases are also called chitinolytic enzymes and catalyze the degradation or hydrolysis of chitin. They are considered an important part of fungal cell walls and serve as an effective defense system against pathogens. Chitinase is an agriculturally important enzyme that is synthesized by various microbes (Chet, 1987). The presence of chitinase in various forms has provided protection to cotton and beans against soil-borne diseases (Ordentlich, Elad, & Chet, 1988; Shapira, Ordentlich, Chet, & Oppenheim, 1989). One of the processes underlying the action that has been exhibited was the lysis activity by chitinase, which resulted in the degradation of the fungal pathogen (Singh, Shin, Park, & Chung, 1999). In the case of application in biological pest control, the enzyme was found to have significant applicability in terms of environmental friendliness, maintenance of soil health, and increasing plant growth and yields (Das & Varma, 2010).

2.8 Proteases

Proteases perform an important function in the mineralization of N in soil. This forms an essential process of regulating the available N for plant growth. Proteases are generally associated with organic and inorganic colloids. The level of activity of these enzymes indicates the biological capability of soil in terms of enzymatic conversion of substrates. The enzyme also serves an essential function in the ecology of microbes in the soil ecosystem (Burns, 1982).

2.9 Ureases

Urease catalyzes the hydrolysis of urea into NH_3 and CO_2, thus raising the pH of the soil in the process. This process results in rapid loss of N to the atmosphere via volatilization of NH_3 (Das & Varma, 2010). Urease also hydrolyzes other compounds such as dihydroxyurea, hydroxyurea, and semicarbazide using Ni as a cofactor (Alef & Nannipieri, 1995). Even though the enzyme is synthesized by various organisms, it is also synthesized by fungi, yeast, and bacteria (Machuca, Cuba-Díaz, & Córdova, 2015). Some of the bacteria that produce urease include *Helicobacter pylori*, *Bacillus pasteurii*, *Staphylococcus* sp., *Providencia* sp., *Klebsiella aerogenes*, and *Proteus mirabilis*, whereas the fungi that release urease include *Schizosaccharomyces pombe* and *Aspergillus* sp. (Krajewska, 2009). The enzyme is greatly distributed in nature. In soil, it occurs both as an intracellular and as an extracellular enzyme and its expression is mostly under the regulation of N (Mobley & Hausinger, 1989). The production of urease is normally stopped during microbial growth when NH_4^+ is used as the main source of N (Geisseler, Horwath, Joergensen, & Ludwig, 2010), whereas the synthesis of urease is initiated when urea or another accessible N source is present (Mobley, Island, & Hausinger, 1995). After urea fertilization, this step is critical for controlling N supply to plants. The activity of urease has gotten a lot of attention as a result of this function since it was first identified in 1935. Various factors influence the activity of urease in soil, including soil amendments, soil depth, heavy metal presence, organic matter concentration, cropping history, and environmental parameters such as temperature. The activity of urease generally increases with increase in temperature, and it was revealed that elevated temperature increases the coefficient of activity of this enzyme. The literature has shown that the activity of urease is easily hampered by elevated concentration of heavy metals (Yang, Liu, Zheng, & Feng, 2006). Therefore, because of its sensitivity and ability to provide information that connects the environmental factors and N cycling, the activity of soil urease has been of great importance and has been used as an index of soil quality. The activity of soil urease can also provide information on the management practices to be adopted, which can enhance the microbial metabolism, cycling of N, and soil fertility (Piotrowska-Dlugosz & Charzynski, 2015).

2.10 Arylsulfatases

These enzymes are widespread in soil. They are released into the external environment by bacteria (*Pseudomonas* sp., *Actinobacteria* sp., *Aerobacter* sp., *Klebsiella* sp., and *Raoultella* sp.) and fungi (*Eupenicillium* sp. and *Trichoderma* sp.) as a response to sulfur deficiency. Their presence in varying soil, in most cases, correlates with the rate of sulfur (S) immobilization and microbial biomass (Kertesz & Mirleau, 2004; Vong, Dedourge, Lasserre-Joulin, & Guckert, 2003). The enzyme induces the digestion of aromatic sulfate esters (R–O–SO_3), sulfate or sulfate sulfur (SO_4^{2-} or SO_4–S), or phenols (R–OH) (Banashree et al., 2017; Tabatabai, 1994a, b). Arylsulfatases are categorized according to the type of ester they hydrolyze. These categories are chondrosulfatases, glucosulfatases, steroid sulfatases, alkylsulfatases, and mycosulfatases (Tabatabai, 1982). Their presence in soil is related to the amount of organic carbon, the rate of microbial biomass, and the rate of S immobilization (Mirleau, Roy, Andrew, & Michael, 2005). Several factors, notably pH shifts, contaminants, and the type and amount of organic materials, influence the activity of these enzymes (Tyler, 1981). Their sensitivity toward these factors serves as an important criterion for using them as an index of soil quality.

3 Mechanisms of Action of Microbial Enzymes in Soil

Soil biota decomposes organic materials in the soil into nutrients that plants require and quickly absorb for optimum growth (Dotaniya et al., 2015; Meena et al., 2016). Soil microbes alter the nutrient kinetics in soil by accelerating the breakdown of compounds in the soil through the release of enzymes. The rhizosphere of roots supplies a significant number of low-molecular-weight organic acids that serve as sources of carbon for microorganisms and have a significant impact on soil enzyme synthesis. As a result, the synthesis of inorganic ions as plant nutrients is expedited (Dotaniya et al., 2014; Meena et al., 2017). In the root zone, the synthesized inorganic ions act as chelating agents, forming temporary complexes with the other plant nutrients. The created complexes then dissolve in the root zones, releasing the enzymes and plant nutrients. Some of the soil enzymes generated break down harmful molecules into innocuous substances, whereas others chelate poisonous ions like metals to prevent their uptake by plant roots (Gianfreda & Rao, 2014). Enzymes require substances to act upon in order to carry out their functions; these compounds are referred to as substrates (Das & Varma, 2011). β-Glucosidase, for example, degrades oligosaccharides with (1 → 4) glycosidic linkages, such as cellodextrins, cellobioses, and cellotrioses, to release glucose molecules. Every enzyme is specific to a substrate or a group of substrates that, under ideal conditions, fit into the active site of the enzyme, resulting in the creation of an enzyme–substrate complex (Das & Varma, 2011; Gianfreda & Rao, 2014). The enzyme catalyzes the reaction in the soil and separates from the products. The enzyme is then free to bind to the next substrate

molecule and catalyze the reaction, resulting in new products. The enzyme undergoes many conformational changes from the initial complex to the ultimate release of the products. Enzymes are absorbed onto clay surfaces and remain active for a long time while being protected from environmental influences like photodegradation (Tietjen & Wetzel, 2003).

4 Factors that Influence the Activities of Soil Microbial Enzymes

4.1 Soil Factors

The activities of soil microbial enzymes are influenced by various factors (Fig. 2), such as changes in temperature. Temperature changes can modify the kinetics of microbial enzymes and the availability of nutrients in the soil (Chatterjee et al., 2019). The activity of soil enzymes increases with increase in temperature. Enzyme activity doubles for every 10 °C rise in temperature within the threshold limit. Above the threshold limit, the activity declines sharply and comes to a cease at extremely

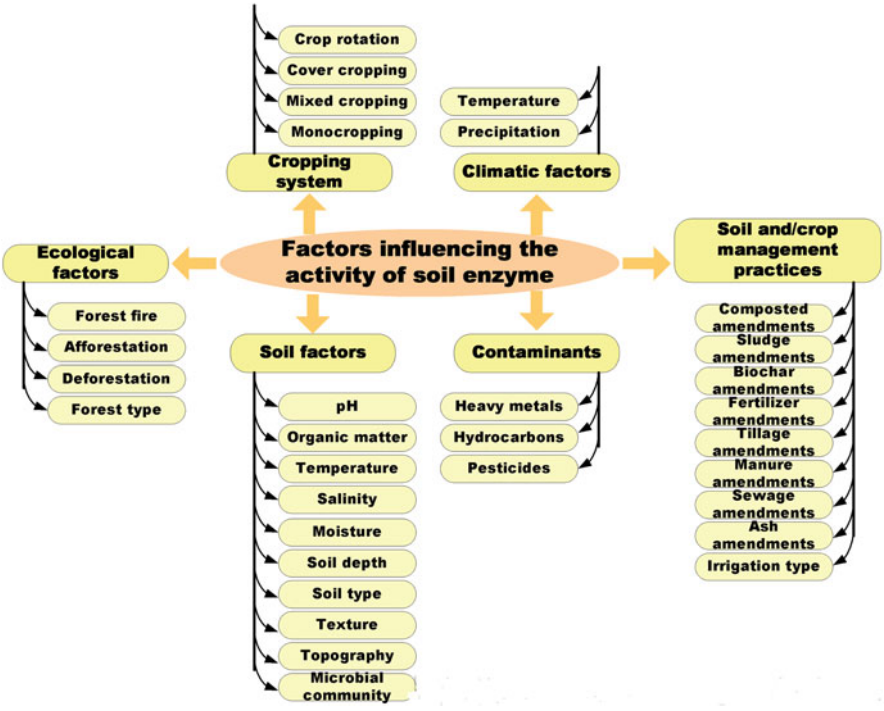

Fig. 2 Factors influencing the activity of soil microbial enzymes

high temperatures; this results in the inactivation of the enzymes (Dotaniya Aparna, Dotaniya, Singh, & Regar, 2019). However, in most cases, the thermal stability of enzymes varies depending on the source and type of enzyme. For instance, thermotolerant microorganisms release enzymes that can perform at a wider range of temperatures. Thermophilic microorganisms release enzymes that are specifically active at an elevated temperature and demonstrate less activity at a lower temperature (Dotaniya et al., 2019). The activities of β-glucosidase, fluorescein diacetate hydrolase, and dehydrogenase have been found to increase with increase in incubation temperature from the surrounding temperature; meanwhile, the activities of arylsulfatase and phosphomonoesterase decreased (Chatterjee et al., 2019). Fang et al. (2016) determined the warming effects on soil enzymes and realized that soil warming had no discernible impact on the activity of cellobiohydrolase, β-glucosidase, and *N*-acetylglucosaminidase; however, it increased the activity of oxidase and decreased the activity of acid phosphomonoesterase.

The salinization of soil, which is either caused by anthropogenic activities or natural factors, has been considered as a serious threat especially in arid and semiarid regions (Guangming et al., 2017; Wichelns & Qadir, 2014). Accumulation of salt has been known to have detrimental effects on the activity of soil microbial enzymes and biochemical processes (Karlen, Tomer, Neppel, & Cambardella, 2008). An increase in the salinity of soil has reportedly resulted in an exponential decrease in the activity of β-glucosidase (Rietz & Haynes, 2003). The activity of β-glucosidase in response to salinity can be utilized as a good indicator of soil quality. For instance, according to Boyrahmadi and Raiesi (2018), the activities of alkaline phosphomonoesterase, β-glucosidase, urease, acid phosphomonoesterase, L-glutaminase, invertase, and arylsulfatase were noticeably low in salinized soils in comparison to controls.

Soil moisture is known to affect microbial metabolism and hence the enzymatic activity in soil. The fact is that the activity of soil enzymes is strongly sensitive to moisture content, coupled with the fact that the moisture influences all the activities and quantities of microbial biomass; therefore, any alteration in soil moisture content will result in an adverse effect on the activity of enzymes, the availability of nutrients, and plant growth (Debouk, San Emeterio, Mari, Canals, & Sebastia, 2020; Steinweg, Dukes, & Wallenstein, 2012). Soil moisture has a significant influence on biochemical processes such as the biotransformation of carbon, which is catalyzed by various enzymes. For instance, when soil moisture was reduced by 10% and 21%, the activity of β-glucosidase was observed to fall by 10–80% and 35–83%, respectively (Sardans & Penuelas, 2005). This shows that the activity and catalytic features of β-glucosidase are influenced by the soil moisture, which results in a slow turnover of nutrients and lowers accessible nutrients to plants.

The depth of soil has an impact on the activity of microbial enzymes. This is closely related to organic matter availability as well as microbial activity. This is because the amount of organic matter in soil reduces as soil depth increases, and, as the amount of organic matter drops, so does the activity of soil microorganisms. This is due to the fact that soil enzyme activity is highly dependent on the availability of substrates and the microorganisms that synthesize the enzymes (Xiao-Chang & Qin,

2006). Many studies have found that the activity of soil enzymes reduces as the depth of the soil increases (Acosta-Martinez, Klose, & Zobeck, 2003; Xiao-Chang & Qin, 2006). The activity of enzymes in a vertical gradient is more pronounced in forest soil than in other ecosystems (Joshi et al., 2018).

The type and texture of soil have shown substantial influence on the activity of enzymes. According to Burns (1982), soil texture performs an important function in the stabilization of soil enzymes. The interactions with clay minerals and soil organic matter particularly affect the enzyme stability (Joshi et al., 2018). In an instance, lower activity of β-glucosidase has been reported in arable soils as compared to meadow and woodland soils (Bandick & Dick, 1999).

Soil enzymes are found to correlate with the abundance of individual microbial groups or microbial diversity (Kaiser, Koranda, Kitzler, Fuchslueger, & Schnecker, 2010). Because soil enzymes are mostly produced by microorganisms, any changes in the microbial community will have a major impact on soil enzyme synthesis (Xu et al., 2021). The enhanced activity of phosphatase in soil treated with mycorrhizal species has been observed in several investigations (Joner & Jakobsen, 1995; Van Aarle & Plassard, 2010). The link between phosphatase activity and mycorrhizal species supports phosphatase's degradative role in soil-bound phosphorus degradation (Van Aarle & Plassard, 2010). Mäder et al. (2011) discovered that amending soil with plant growth-promoting bacteria and arbuscular mycorrhizal fungi boosts the activities of dehydrogenase, urease, and phosphatase, resulting in improved soil quality. According to Wu, Wan, Wu, and Wong (2012), the presence of nitrogen-fixing bacteria increased the activities of phosphatase and urease. Furthermore, Xu et al. (2021) discovered a positive correlation between the soil bacterial community and the activity of β-1,4-glucosidase, which is engaged in C transformation, and a positive correlation between the fungi and the activity of oxidase, which is involved in C oxidation.

4.2 Climatic Factors

Precipitation and temperature are important climatic factors that influence the microbial communities and activities of enzymes in terrestrial ecosystems (Baldrian, Šnajdr, & Merhautová, 2013). Fluctuations in soil moisture and temperature occur seasonally, and the seasonal dynamics of microbial composition in soil are greatly related to the seasonal shifts in soil moisture and temperature (Rasche, Knapp, & Kaiser, 2010). Climatic factors are known to influence the microbial communities as well as the activities of their enzymes (Lanzen et al., 2016). This also results in affecting the fertility of the soil. In a study conducted by Sardans and Penuelas (2005), a decrease in precipitation had resulted in the reduction of β-glucosidase activity by 10–80%, protease by 15–66%, and urease by 10–67% while the further absence of moisture had resulted in a decline in 35–54%, 42–60%, 31–40%, and 35–83% of the activities of protease, urease, β-glucosidase, and acid phosphatase, respectively. Moreover, the activities of urease and protease were affected by

drought (Sardans & Penuelas, 2005). On the other hand, about 33–80% reduction of laccase, peroxidase, and chitinase activities has been reported in soil samples collected during winter with a temperature of about 0 °C as compared to those collected during autumn when the temperature was around 15 °C. This shows that seasonal temperature can significantly influence the activity of microbial enzymes in soil ecosystems (Joshi et al., 2018). Zi, Hu, and Wang (2018) realized that short-term climatic changes can enhance the mineralization of plant nutrients and change the activity of soil enzymes in alpine meadow ecosystems. Some research found relatively higher activities of enzymes in the soil in colder environments (Jing, Wang, & Chung, 2014); meanwhile, other findings have reported substantial activities of soil enzymes during warmer periods (Baldrian et al., 2013; Jing et al., 2014). This implies that the relationships may differ in specific climatic zones (Luo He, Zeng, Li, & Yang, 2020).

4.3 Contaminants

The presence of contaminants in soil affects microbial metabolism, growth, and reproduction and eventually disrupts biochemical activities such as enzymatic activities. Contaminants can exert direct effects on enzyme activity, thereby destroying the spatial structure of enzyme active groups. For instance, the inhibition of invertase activity by contaminants has been revealed by many researchers, and most asserted that soil contaminants have a significant influence on microbial communities and soil respiration and have negative interactions with soil enzymes (Peyrot, Wilkinson, Desrosiers, & Sauvé, 2014; Tripathy, Bhattacharyya, Mohapatra, Som, & Chowdhury, 2014). The activities of enzymes can be altered by an elevated concentration of toxic metals (Duan et al., 2018). As the concentration of metal increases, the activities of most enzymes decrease drastically (Tripathy et al., 2014). The activity of dehydrogenase (38.9–18.1 g triphenylformazan/g soil/24 h), alkaline phosphatase (80.7–64.0 g p-nitrophenyl phosphate (PNP)/g soil/h), and acid phosphatase (73–55 g PNP/g soil/h) all decreased significantly as Pb concentrations increased from 0 to 300 mg/kg of soil (Dotaniya & Pipalde, 2018). Cao et al. (2020) revealed that the activities of urease, invertase, and cellulase decreased by 55.0–76.7%, 28.5–59%, and 17.3–34.1%, respectively, following an increase in the concentration of Cu. Hassan et al. (2020) revealed negative correlations between the concentrations of Cr, As, Cu, Mn, and Fe in landfill soil and the activities of urease and dehydrogenase. The application of pesticides to agricultural soils has resulted in several effects (positive and negative) on enzyme activities. The negative effects on enzymes such as oxidoreductases, hydrolases, and dehydrogenases have been broadly reported (Menon, Gopal, & Parsad, 2005; Monkiedje, Ilori, & Spiteller, 2002). The presence of high levels of crude oil and other heavy oil fractions can inhibit enzyme function by covering cell surfaces and organo-minerals, keeping soluble substrates away from enzyme molecules. According to Wang, Zhan, Zhou, and Lin (2010), the threshold level for activating or inhibiting the activities of

dehydrogenase, phosphatase, and urease was 1000 mg/kg of mixed residual hydrocarbons. The toxic effects of some of the contaminants on the enzyme activities are depicted in Table 1.

4.4 Cropping System

The cropping system has been found to influence the activity of soil enzymes in different ways. For instance, phosphatase activity was found to be high under a crop rotation system involving meadow and oats, whereas under a monoculture system with soybean or corn, the activity was lower (Dodor & Tabatabai, 2003). In South African alluvial soil, Mukumbareza, Chiduza, and Muchaonyerwa (2015) discovered that rotating *Zea mays* with vetch and fertilized oat cover crop enhanced phosphatase activity and microbial biomass. The increased activity of phosphatase and microbial biomass in bicultures than in monocultures indicated the synergistic effects of the cover crops in the bicultures and can serve as a valuable avenue for enhancing the soil physicochemical properties and P cycling (Mukumbareza, Muchaonyerwa, & Chiduza, 2016). According to Chen, Guo, Guo, Tan, and Wang (2021), the increased duration of monocultures has reportedly decreased the activity of β-glucosidase, whereas, on the other hand, the activities of alkaline phosphatase and nitrate reductase increased nonlinearly. Extended monocultures of tea bush and tomato have reduced the microbial metabolic and enzymatic activities and resulted in shifts in the composition and structure of microbial communities (Fu et al., 2017; Li et al., 2017). Mganga, Razavi, and Kuzyakov (2016) realized that the fertility of the soil, the activity of the associated enzyme, and soil microbial biomass were enhanced in soil under traditional agroforestry systems than under monocropping with maize under the neutral to slightly acidic soil of tropical Africa.

4.5 Soil and/or Crop Management Practices

It is critical to understand the impact of various management strategies on the activity of enzymes in soil in order to improve soil quality and productivity. The activity of soil enzymes may be influenced by agricultural management practices. The activities of microbial enzymes and soil quality are altered by soil amendments under various management systems (Table 2). For example, when organic fertilizers such as sewage sludge, plant residues, compost, manure, and vermicompost were used, the activities of acid and alkaline phosphatase rose (Nannipieri et al., 2011; Piotrowska-Dlugosz & Wilczewski, 2014). Simultaneous addition of municipal solid waste or vermicompost and mineral N fertilizers has resulted in a higher activity of phosphatase than the application of individual fertilizers (Srivastava et al., 2012). Piotrowska-Dlugosz and Wilczewski (2014) revealed that the activity of phosphatase increased when soil containing low organic matter was supplemented

Table 1 Effects of contaminants on the activity of soil enzymes

Enzymes involved	Type of soil	Contaminant	Dosage of contaminant applied	Effect on soil enzymes	References
Dehydrogenase and phosphatase	Field soil	Kerosene and diesel	Kerosene (1% v/w) and diesel (1% v/w)	Inhibited the activities of the enzymes	(Alrumman et al., 2015)
Dehydrogenase, catalase, acid and alkaline phosphatase, and urease	Agricultural soil	Chlorothalonil	Chlorothalonil: 0.00, 1.660, and 16.60 mg/kg dry matter of soil	Inhibited the activity of dehydrogenase, catalase, and acid phosphatase	(Bacmaga, Wyszkowska, & Kucharski, 2018)
Invertase, urease, and cellulase	Paddy soil	Cu	Cu: 150 and 450 mg/kg soil	The activities of invertase, urease, and cellulase decreased by 28.5–59%, 55.0–76.7%, and 17.3–59%, respectively	(Cao et al., 2020)
Dehydrogenase, acid phosphatase, and alkaline phosphatase	Vertisol soil	Pb and Ni	0, 100, 150, and 300 mg/kg each for Pb and Ni	The activity of dehydrogenase decreased to 38.9, 32.1, 30.9, and 18.1 μg triphenylformazan/g soil/24 h at 0, 100, 150, and 300 mg/kg, respectively The activity of acid phosphatase decreased to 73, 61, 58, and 55 μg PNP/g soil/h at 0, 100, 150, and 300 mg/kg, respectively The activity of alkaline phosphatase decreased to 80.7, 69.4, 66.2, and 64.0 μg PNP/g soil/h at 0, 100, 150, and 300 mg/kg, respectively	(Dotaniya & Pipalde, 2018)

Invertase and β-glucosidase	Soil from uranium mining sites	As, Au, Cd, Cr, Cu, Mo, Ni, Pb, Sr, V, Zn, and U	Various treatments and dosages	The activities of the enzymes decreased with increase in metal concentrations and radiation	(Yang et al., 2018)
Fluorescein diacetate, β-glucosidase, and protease	Sediments	Cr, Cd, Cu, Ni, Pb, and Zn	Cd: 0.00–0.30 μg/g sediments Cu: 0–60 μg/g sediments Cr: 0–150 μg/g sediments Ni: 0–70 μg/g sediments Pb: 0–60 μg/g sediments Zn: 0–130 μg/g sediments	Enzyme activities negatively correlated with metal concentrations	(Jaiswal & Pandey, 2018)
Peroxidase and catalase	Field soil	Pesticides: dithiocarbamate, avermectin, organochlorine, and chlorothalonil	10 mL aqueous solution	The activities of the enzymes were affected negatively and positively	(Micuti, Badulescu, Burlacu, & Israel-Roming, 2018)
Protease, urease, dehydrogenase, and catalase	Agricultural soil	Pesticide: *cis*-nitromethylene neonicotinoid	20 mg/kg soil	Urease was initially inhibited	(Cai et al., 2016)

Table 2 Influence of different types of soil amendments on the activity of soil microbial enzymes

Enzymes involved	Type of soil amended	Material used for the amendment	Dosage/concentration applied	Effect of treatment on the activity of soil enzymes	References
Dehydrogenase, alkaline phosphatase, and urease	Agricultural soil	Sewage sludge	5, 10, 20, 30, and 50 t/ha	Increase the activity of the enzymes for up to 50–55%	(Dhanker, Chaudhary, Goyal, & Kumar, 2020)
β-glucosidase, β-D-cellobiosidase, β-xylosidase, *N*-acetyl-β-glucosaminidase, phosphatase, and leucine aminopeptidase	Aridisol soil	Biochar and dry manure	Biochar: 22.4 mg/ha and dry manure: 42 mg/ha	Biochar had no effect Dry manure had no effect Biochar + dry manure increased the activities of the enzymes	(Elzobair, Stromberger, Ippolito, & Lentz, 2016)
β-glucosaminidase, arylsulfatase, β-glucosidase, and acid phosphatase	Sandy soil	Biochar	5%, 10%, 0% v/v	Increased the activity of β-glucosaminidase by 5–30% and arylsulfatase by 12–46% Decreased the activity of β-glucosidase by 18–35% and acid phosphatase by 5–22%	(Frene et al., 2021)
Dehydrogenase, phosphatase, β-glucosidase, and urease	Agricultural soil	Poultry litter and biochar	Poultry litter: 70 kg N/ha biochar: 20 t/ha) poultry litter + biochar: 70 kg N/ha poultry litter and 20 t/ha biochar	Increased the activity of the enzymes	(Gao, Hoffman-Krull, & DeLuca, 2017)
Dehydrogenase, protease, β-glucosidase, and phosphomonoesterase	Agricultural soil	Organic pruning, manure, legume cover crop, and inorganic fertilizer	Organic pruning + manure: 0.63% N, 0.27% P_2O_5, 0.81% K_2O at a rate of 20 mg/ha Organic pruning + legume cover crop Inorganic fertilizer NPK: 8/4/12 at a rate of 250 kg/ha/year	Increased the activities of the enzymes	(Garcia-Orenes et al., 2016)

Dehydrogenase, β-glucosidase, fluorescein diacetate, cellulase, urease, protease, arylsulfatase, alkaline phosphatase, peroxidase, and phenoloxidase	Agricultural soil	Mineral fertilizers and organic fertilizers	Mineral fertilizers as used by farmers Recommended dose of mineral fertilizers: 50% inorganic + 50% organic 25% inorganic + 75% organic 75% organic + innovative 100% organic	Enzyme activities increased (50–75%) significantly in response to organic amendments	(Ghosh et al., 2020)
Urease, alkaline phosphatase, and catalase	Coastal saline soil	Hekang (soil modifier), chemical fertilizers, microbial inoculants, and organic fertilizers	Hekang: organic polymer Chemical fertilizers as NPK Organic fertilizer: organic matter (30%), NPK (8%) in the ratio of N: P: K = 3:2:3 Microbial inoculum: number of effective viable cells $\geq 10^{10}$/g	Enzyme activities improved by different amendments	(Guangming et al., 2017)
β-glucosidase, α-glucosidase, β-cellobiosidase, β-xylosidase, and *N*-acetyl-β-glucosaminidase	Paddy soil	Mineral fertilizers (NPK), organic fertilizers (livestock manure), and wheat straw	NPK: N, 351.75 kg/ha; P_2O_5, 75 kg/ha; K_2O, 84 kg/ha NPKM: N, 282.75 kg/ha; P_2O_5, 75 kg/ha; K_2O, 84 kg/ha) + livestock manure, 1500 kg/ha NPKS: N, 351.75 kg/ha; P_2O_5, 75 kg/ha; K_2O, 84 kg/ha + wheat straw, 3000 kg/ha	Activities of enzymes were enhanced	(Guo et al., 2018)

(continued)

Table 2 (continued)

Enzymes involved	Type of soil amended	Material used for the amendment	Dosage/concentration applied	Effect of treatment on the activity of soil enzymes	References
β-glucosidase, urease, and phosphodiesterase	Acidic tropical soil	Biochar and fertilizers	Palm kernel shell biochar (20 t/ha) Rice husk biochar: 20 t/ha Palm kernel shell biochar + fertilizer: 20 t/ha Rice husk biochar + fertilizer: 20 t/ha Fertilizer alone Control	All amendments significantly improved the enzyme activities	(Halmi, Hasenan, Simarani, & Abdullah, 2018)
β-glucosidase, urease, arylsulfatase, dehydrogenase, and acid and alkaline phosphatase	Agricultural soil	Inorganic fertilizers (NPK) and organic fertilizers	NPK: N, 2.4–2.7 kg/m/year; P, 0–12.6 kg/m/year; K, 0–0.6 kg/m/year Organic fertilizer: 9.4–10.5 kg/m/year	Organic fertilizers enhanced the activities of alkaline phosphatase, β-glucosidase, arylsulfatase, urease, and dehydrogenase by 41%, 26%, 47%, 39%, and 41%, respectively	(Igalavithana et al., 2017)
β-glucosidase, urease, acid phosphomonoesterase, and dehydrogenase	Agricultural soil	Olive pomace	Olive pomace: 50 mg/ha	The activities of enzymes in the treated plot were significant from those of the controls (without amendment)	(Innangi et al., 2017)
β-glucosidase, urease, acid and alkaline phosphatase, dehydrogenase, arylsulfatase, cellulase, and phenol oxidase	Agricultural soil	Biochar	0%, 15%, 20% w/w	Enhanced the enzyme resistance	(Jain et al., 2016)

Catalase, sucrase, and urease	Agricultural soil	Herbicide (acetochlor)	50%	The herbicide did not affect the activity of enzymes at first sampling	(Jiang et al., 2017)
β-glucosidase and urease	Agricultural soil	Biochar and fertilizers (NPK)	Biochar: 0 mg/ha + NPK: 32 kg/ha:14 kg/ha:16 kg/ha Biochar: 3.125 mg/ha + NPK: 32 kg/ha:14 kg/ha:16 kg/ha	The activities were significant than in controls	(Kaewpradit & Toomsan, 2019)

with P fertilizers, whereas there was no change in the activity of phosphatase when soil with high organic matter was also amended with P fertilizers. Other studies have revealed that amendments of soil with a combination of fertilizer treatments with vermicompost, compost, straw mulch, and municipal solid waste compost have resulted in increased activity of β-glucosidase than those without any compost and those supplemented with herbicides and synthetic fertilizers (Crecchio, Curci, Pizzigallo, Ricciuti, & Ruggiero, 2004; Meyer, Wooldridge, & Dames, 2015). Treatment of mining soil with biosolids in combination with a plant resulted in a substantial ($P < 0.05$) increase in β-glucosidase, alkaline phosphatase, and urease activities (Cele & Maboeta, 2016). Long-term irrigation with treated papermaking effluents, on the other hand, resulted in a considerable increase in urease, polyphenol oxidase, and invertase activities when compared to controls (Chen, Liang, Chen, Yang, & Ding, 2016). According to Pandey, Agrawal, and Bohra (2014), a reduction in the frequency of tillage in the no-tillage system had resulted in increased activity of β-glucosidase as compared to the conventional tillage system. In their study, Dominchin, Verdenelli, Aoki, and Meriles (2020) revealed that soil that was subjected to moderate water erosion had reduced microbial activity; meanwhile, the activity of dehydrogenase was increased. Furthermore, the activity of glucuronidase had reduced in the soil subjected to moderate water erosion.

4.6 Ecological Factors

Various ecological factors are known to affect the activity of soil enzymes. Soil enzymes and their relationships with ecological factors have received much attention in recent years (Ladwig, Sinsabaugh, Collins, & Thomey, 2015; McDaniel, Kaye, & Kaye, 2013; Zheng et al., 2018). Natural forest systems that have been transformed into agricultural fields have an impact not only on the plants but also on the soil's biological features. For instance, higher activities of β-glucosaminidase, β-glucosidase, phosphatases, arylamidase, arylsulfatase, and phosphodiesterase were observed in native grassland, rotation with other crops, and conservation reserves than with continuous cotton (Acosta-Martinez et al., 2003). According to Sicardi Garcia-Prechac, and Frioni (2004), conversion of natural grazed pastures to commercial plantations had significantly affected the activities of alkaline and acid phosphatase, dehydrogenase, soil respiration, and C mineralization. On the other hand, deforestation and afforestation are also found to influence the activity of soil enzymes. They are known to affect the quality of soil as compared to undisturbed soil. According to Bastida, Moreno, Hernandez, and Garcia (2006), the activities of protease and dehydrogenase were lower in deforested soil than in undisturbed soil. Furthermore, Izquierdo, Caravaca, Alguacil, Hernández, and Roldán (2005) claimed that removing vegetation had long-term negative consequences for soil microbial and metabolic activity. They further added that even after 15 years of deforestation, the soil quality has not improved. On the other hand, however, they realized that the activities of protease, urease, acid phosphatase, and β-glucosidase were higher in the

soil after 4 years of revegetation (Izquierdo et al., 2005). Forest fire is regarded as a natural occurrence that causes numerous negative effects on soil ecosystems (Karaca, Cema, Turgay, & Kizilkaya, 2011). When there is a forest fire, most of the N found in soil and biomass escape into the atmosphere due to the low volatilization temperature of N. The effects of fire on the ecosystem are only differentiated by the activities of a few enzymes. The activities of various enzymes have been examined for differentiating the effects of fire-related stress on soil quality, and they have been found to increase or decrease (Karaca et al., 2011). For instance, the activities of protease and invertase were found to decline with burning, whereas the activities of peroxidase, polyphenol oxidase, and acid phosphatase increased (Zhang, Wu, Zhou, & Bao, 2005).

5 Conclusions

Soil microbial enzymes represent an important parameter for the quality of soil and plant well-being. Most of the degradative activities in soil are catalyzed by soil microbial enzymes. This provides essential sources of nutrients to the soil, thereby improving the fertility of the soil. The activities of soil enzymes are affected by various factors; this provides various signals regarding the status of the soil quality. It is therefore important that regular monitoring of the activity of soil enzymes should be put in place as it will give room for early correction of the soil condition. This will ensure effective maintenance of the quality and fertility of the soil.

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