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SIGNIFICANCE OF SOIL ENZYMES IN NUTRIENT TRANSFORMATIONS

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A b s t r a c t: Soil is a heterogeneous system in which different phases and numerous components are involved in physical, chemical and biological processes. The dynamic nature and complex chemistry of soil organic matter make it a major source of plant nutrients. The movement of materials among the biotic and abiotic portions of soil environment is catalysed largely by soil enzymes. The paper comprises the basic information about the origin, localization and the role of soil enzymes in nutrient transformations. The influence of soil air-water conditions on enzyme activity was marked.

K e y w o r d s: soil, enzyme activity, nutrient transformation.

INTRODUCTION

The primary function of the soil is related directly to its biomass, which, as a continually cycled pool of nutrients is the prerequisite for the growth of plants. For the nutrients to be taken up, organic matter entering the soil has to be degraded to inorganic components. This degradation is brought about by the indigenous microbiological activity of soil. During the decomposition and synthesis of organic substances in the soil, the metabolism and energy exchange proceed with the participation of the enzymes. As a result of the enzymatic processes in the soil, the difficulty assimilated nutrient compounds are converted into the forms, which are easily available to plants and microorganisms. Consequently, the development of soil fertility is closely associated with enzymatic processes and the manifold and multistep processes of mineralization and immobilization of organic constituents represent the link between the soil and the global carbon and nutrient cycles [22,73].

ORIGIN AND LOCALIZATION OF ENZYMES IN SOIL

Soils harbor numerous organisms - bacteria, actinomycetes, fungi, microalgae, protozoa, nematodes, earthworms and other invertebrate microfauna - mostly arthropods

(crustaceans and insects), ascari and mollusks [50]. Soil enzyme activity is produced primarily by microorganisms (e.g. bacteria, fungi), but also originated from animal and plant sources (e.g. roots, lysed plant residues, digestive tracts of small animals) [45]. Some enzymes may originate in part from plant remains while others may be synthesised almost entirely by soil organisms. Macroscopic animals, including earthworms, arthropods and vertebrates are important in soil biology as well, but are on the scale larger than the microhabitat and their contribution to overall soil enzyme activity is difficult to estimate [10].

The possible localization of enzyme activities in soil illustrates Fig. 1. The endoenzymes may exist in living cells in different cellular compartments, such as the cytoplasm or periplasm, or they may be associated with the cell membrane and/or cell wall. Extracellular enzymes are produced and secreted by living cells and operate at a distance from the parent cell, either as free enzymes in the liquid phase, or as enzymes still associated with the external surface of root epidermal or microbial cell wall (i.e. partially attached to or trapped within a viscous network of homo- and heteropolysaccharides secreted by several cells which still allow the passage of substrate and products [23]). Components of the enzyme activity of soil

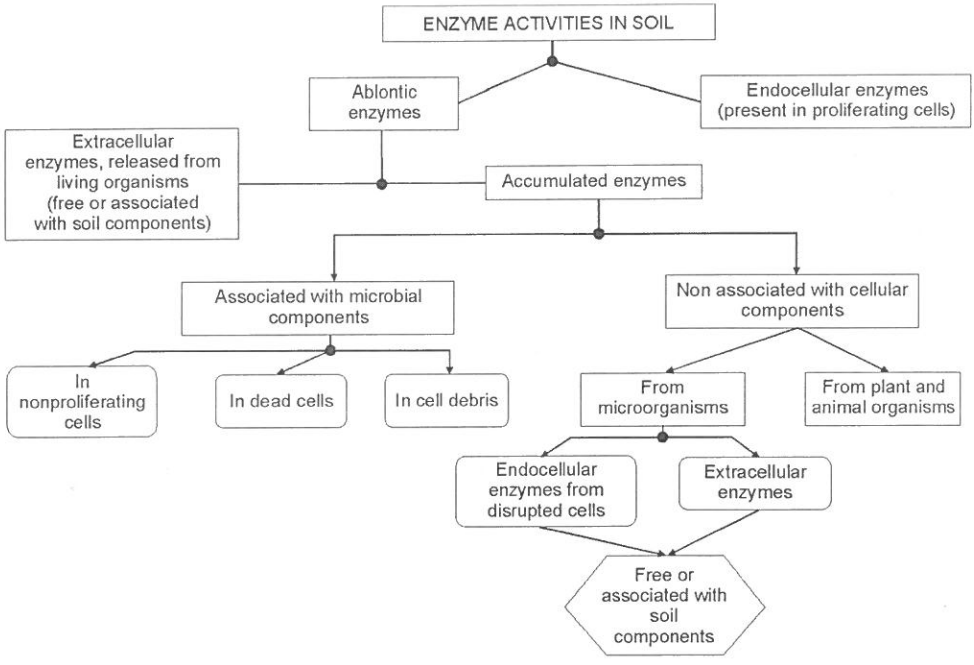

Fig. 1. Localization of enzyme activities in soil (From Gianfreda and Bollag [23]).

were classified first by Kiss et al. [40] and subsequently by Skujins [71]. Burns [8] divided the overall enzymatic activity of soil into 10 reasonably distinct categories and this clear and precise classification includes that of Kiss and Skujins. In fact, individual enzymes may belong to more than one category and may change from one to another with time. Some of the enzymes (e.g. urease and β-glucosidase) catalyse reactions both inside and outside of the organisms that synthesised them; some of the cellulases and proteinases can only function outside of the producing cells because of their large size of their target substrate; and others (e.g. dehydrogenases and nitrate reductase), being involved in the central aspect of metabolism, do not function extracellularly [23].

Free enzymes are believed to be short-lived in soils, being vulnerable to degradation and to immobilization on the surfaces of soil clay and organic colloids (Fig. 2). Immobilization, being the norm in the soil environment [7,8,45,46,66], protect enzymes against degradation and denaturation, and retain their activity for a long time, usually at the cost of some loss of activity. These stabilized enzymes can be active also in the absence of proliferating and nonproliferating microorganisms. Thus, the overall activity of any enzyme in soil is the result of activities associated with enzymes at different sites [14].

RANGE OF SOIL ENZYMES

Studies on different enzyme activities in soil are important as they indicate the potentiality of soil to carry out all the biochemical processes, which are important to maintain the soil quality and fertility. Many reviews have discussed the properties of enzymes in soil and correlation between particular enzyme activity and different soil properties [1,3,12,18,30,37,40,41,43,44,49,51,52,66,70].

Assays have been devised for a wide range of soil enzymes that are representative most of the enzyme classes. Oxidoreductases and hydrolases have been the most studied because of their role in organic matter degradation and release of nutrients. Few studies have been concerned with the activities of transferases (e.g. transaminase, rhodanese) and lyases (e.g. decarboxylases) [71].

Oxidoreductases

Dehydrogenases catalyse a broad range of reactions of degradation (dehydrogenation) of organic matter. Numerous soil dehydrogenases are assumed to function only intracellularly, exclusively associated with live, intact cells. Dehydrogenase activity has been used as a general index of soil biological activity because of the involvement of

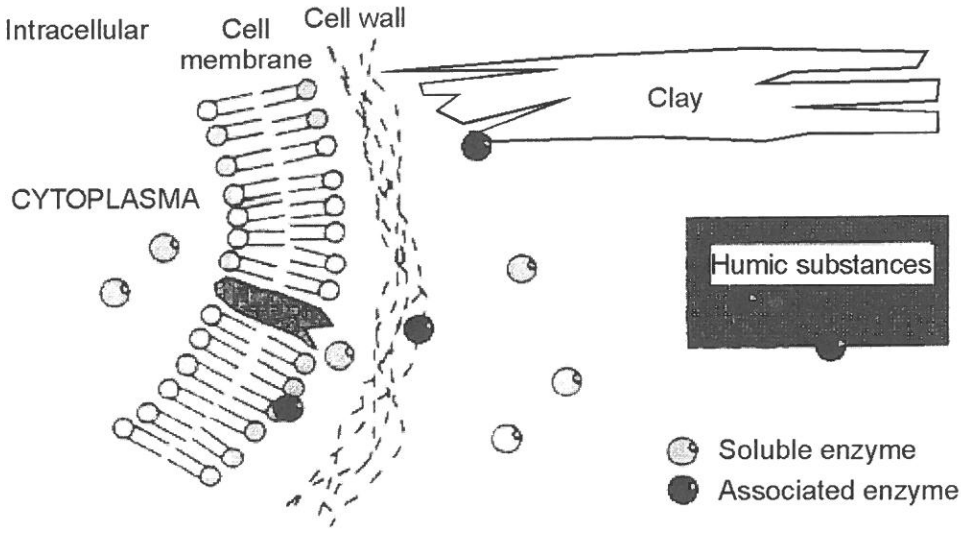

Fig. 2. Distribution of "extracellular" enzymes in soil (From Dilly and Nannipieri [14]).

these enzymes in the oxidative energy-transfer sequences [46]. Numerous studies reveal correlations of the activity with several biomass parameters such as microbial numbers, soil respiratory activity, ATP content, other enzyme activities, carbon and nitrogen cycling, organic matter content [3,10,52,67].

Catalase catalyse decomposition of hydrogen peroxide, formed during aerobic respiration as a by-product, thus playing an important detoxifying role because of the extreme reactivity of H_2O_2 and possibility of irreversible damage of biomolecules. Catalase is one of the most efficient enzymes known. It is produced by aerobes and most of the facultative anaerobes [32,7].

Peroxidases, catalysing the oxidation of substrates in the presence of H_2O_2, are involved in the degradation of lignin and phenols [38].

Phenoloxidases oxidise phenols, generated during degradation of lignin or microbial synthesis [38]. The group includes o-diphenol oxidase (tyrosinase), p-diphenol oxidase (laccases) and polyphenol oxidases. These enzymes are apparently involved in humification processes [71].

Hydrolases

Amidases (acylamide amidohydrolases), catalyse the hydrolysis of amides (C-N bonds) to ammonia and the corresponding carboxylic acid. Amidases are common enzymes, accumulated in soil [12,21,67].

Amylases (α- and β-amylases) hydrolyse starch and related oligo- and polysaccharides containing glucose units. β-Amylases are more active. Both the forms are accumulated in the soil. Starch (consisting of two glucose polymer, amylose and amylopectin) is the major food reserve of plants. α-Amylase degrades both amylose and amylopectin to units consisting of several glucose molecules. β-Amylase reduces amylose to maltose. Amylopectin is degraded to a mixture of maltose and dextrin. Many bacteria and fungi degrade starch [57,63].

L-Asparginase and **L-Glutaminase** hydrolyses L-asparagine and L-glutamine to L-aspartic and L-glutamic acids, respectively, and NH_3. These intra- and exracellular enzymes are widely distributed in nature and have an important role in nitrogen mineralization in soils [19,20,21].

Cellulases catalyse the hydrolysis of the β-1,4-glucan bonds of cellulose to D-glucose. This biochemical activity is an interaction of three enzyme groups: endo-β-1,4-glucanases, exo-β-1,4-glucanases (cellobiohydrolases) and β-glucosidases (cellobiases) [1,15,45,57]. Extracellular cellulases bind to the crystalline substrate and cleave cellulloligosaccharides from the non-reducing ends, intracellular enzymes cleave glucosidic linkage along non-crystalline parts of cellulose substrate, while β-glucosidases release glucose from cellulloligosaccharides and aryl-β-glucosides. Cellulose, the most abundant structural polysaccharide of plant cell walls, is nearly always associated with hemicellulose and lignin. The degradation of cellulose in soils is a slow process, depending on environmental factors and activity of soil microorganisms. Soil cellulases are mainly produced by fungi, but also by a few species of actinomycetes and some anaerobic Clostridium [9]. Hemicelluloses are the heterogeneous group of compounds polymers of hexoses and pentoses. In nature hemicelluloses are complexed with other substances that make the breakdown difficult. The process involves the action of pectinases. Fungi appear to initiate the degradation of hemicelluloses and actinomycetes can maintain the attack over a prolonged period. Hemicelluloses are generally considered to be degraded faster than cellulose, probably as a result of a grater number of microorganisms using these compounds as a substrate [33,57].

Chitinase and chitobiase catalyse the hydrolysis of chitin to acetyl glucosamine. Chitin, one of the major contributors of amino sugars in soil, is the components of fungal cell walls [1].

Glucanase (β-1,3-glucan glucanohydrolase, laminarinase), present as exo- and endocellular enzyme, hydrolyses β-glucan component of cell wall [67].

Glucosidases. β-Glucosidases (called as cellobiases, gentobiase, emulsin) exist in extra- and intracellular forms and are the rate limiting enzymes in the microbial

degradation of cellulose to glucose. α-Glucosidase (maltase), β-galactosidase (lactase) and α-galactosidase (melibiase) are also included among glucosidases [1,8,71].

Ligninase. Lignin is slowly catabolised to CO_2, but very little lignin C is found in microbial biomass, whereas 70 % or more was being stabilised in the soil [78]. The biodegradation of lignin, with its phenylpropanoid units irregularly connected by C-O-C and C-C linkages, is less understood than that of cellulose. Lignin is formed as an encrusting material on the cellulose and hemicellulose matrix and does not show a specific order [33,57]. The most active biodegraders of lignin belong to the white-rot fungi, present mostly in forest, not arable, soils. In arable soils, lignocelluloses are probably degraded by synergistic consortia of microbes (Fungi Imperfecti, the actinomycetes and bacteria). None of the organisms yet isolated can use lignin as a sole C source [33]. The enzymes involved in lignin degradation are lignin peroxidases (ligninase), manganese peroxidases, lignase, laccases, and glucose oxidases [33,48,57,69].

Lipase (triacylglicerol acylhydrolase, classified also as carboxylic ester hydrolase, aryl esterase, glycerol ester hydrolase) hydrolyses the initial step of degradation of lipids to fatty acids and glycerol [1,38].

Phosphatases represent a broad range of intracellular as well as extracellular enzymes that catalyse the hydrolysis of phosphate esters [67]. These enzymes exhibit rather broad specificity, capable of acting on a numerous of different structurally related substrates at different rates. They include phosphoric monoester hydrolases (i.e. nucleotidases, phytase, sugar phosphatases and glycerophosphatase), phosphoric diester hydrolases (nucleases, phospholipases), triphosphoric monoester hydrolases, and enzymes hydrolyzing P-N bonds, such as phosphoamidases. Phosphomonoesterases are enzymes extensively studied because of their role in hydrolysing of organic phosphomonoester to inorganic phosphorus, which can be taken up by plants. According to the optimum pH, phosphomonoesterases are classified as acid, neutral and alkaline phosphatases [2,3,67].

Proteases catalyse the hydrolysis of proteins to polypeptides and oligopeptides to amino acids, which are further transformed to ammonium and nitrate. The first step of protein degradation is extracellular because of the high molecular weight of proteins. Proteolytic activity in soil is an important part of the N cycle. Proteins, amino acids, amino sugars, amides and nucleic acids (from plant residues and dead microbial cells) are generally readily degraded by many soil microorganisms via proteolytic enzymes that hydrolyze the peptide links (pronase, proteases, peptidases, amidohydrolases). In soil, proteases are present in living, active cells,

in dead cells, as free enzymes and adsorbed to organic, inorganic and organo-mineral particles [1,10,33,47].

Saccharase (β-fructosidase, invertase) catalyses the hydrolysis of sucrose to D-glucose and D-fructose [63].

Sulphatases include enzymes of the mineralization of organic sulphate esters in soil. There are numerous sulphatases, bound to the cell walls or present in the periplasm. Production of arylsulphatases and choline sulphatase is repressed in the presence of available SO_4^{2-} [3,57,67].

Urease catalyses the hydrolysis of urea to CO_2 and NH_3. This enzyme is very widely distributed in nature. Urease is accumulated in soil to a significant extent and is tightly bound to soil organic matter and soil minerals. Because of the agricultural importance of urease as a decomposing agent for urea, which is used as a fertiliser, urease has been widely studied. Urease activity of soil is considered to be due mainly to enzyme located extracellularly [1,12,45,67].

Xylanase acts on β-1,4-xylans present as cell wall constituents of plants. Activity of xylanase includes exoxylanases, which catalyse the hydrolysis of xylans to oligosaccharides, and endoxylanases, catalysing hydrolysis of oligosaccharides to reduced monomers [1,67,68].

SOIL ORGANIC MATTER TRANSFORMATION

The dynamic nature and complex chemistry of soil organic matter makes it a major source of plant nutrients in terrestrial ecosystems. SOM contents range from less than 0.2 % in desert soils to over 80 % in peat soils. With 95 % of soil nitrogen (N), 40 % of soil phosphorus (P) and 90 % of soil sulfur (S) being associated with the SOM fraction, decomposition and turnover can supply most macronutrients needed for plant growth. During decomposition, heterotrophic microorganisms assimilate complex organic substances for energy and carbon (C) and release inorganic nutrients. The special role in nutrient cycling play autotrophic microorganisms which, like higher plants, assimilate CO_2 as well as N_2-fixing bacteria. In fact, in soil exist various phototrophs, chemotrophs, litotrophs and organotrophs [42]. The processes of soil organic matter transformation are controlled by temperature, moisture, soil disturbance, as well as by the quality of SOM as a microbial substrate [72]. The close relationships between C availability, activity of soil biomass and nutrient transformations have been established in both laboratory and field experiments. Specific ^{14}C-, ^{15}N-, ^{32}P- and ^{35}S - labelled compounds (including that in plant residues) have been used to describe the degradation of added materials to the soil [52].

SOM transformations begin with the decomposition of fresh plant residues (applied or deposited naturally). Plants contain 15-60% cellulose, 10-30% hemicellulose, 5-30% lignin, 2-15% protein and up to 10% soluble materials (such as sugars, amino sugars, organic acids and amino acids) [33,56]. Plant residues, freshly incorporated into topsoils, are quickly colonised by a variety of microorganisms. In addition to rhizospheres, decomposing organic particles represent concentrations of biological activity in the soil matrix ("hot spots" of activity) [46]. Under suitable conditions of pH, temperature, and moisture content, plant residues are extensively degraded within a few months [17,35]. Most of the plant residue is decomposed in the first year, releasing a significant amount of plant nutrients, and C as CO_2. The remainder decomposes more and more slowly with time and becomes steadily incorporated into soil humus [33,56].

A simplified soil organic matter-cycling diagram illustrates Fig. 3 [72]. During plant matter decomposition, complex compounds are broken down to simpler compounds that can be utilised by the microorganisms. A part of the polysaccharides is depolymerised to disaccharides and then hydrolysed to simple sugars. The more chemically complex compounds undergo a series of catalysed reactions, performed by more than one microbial species. The humified SOM is slow decomposable material that is complexed, to various degrees, with the mineral fraction of

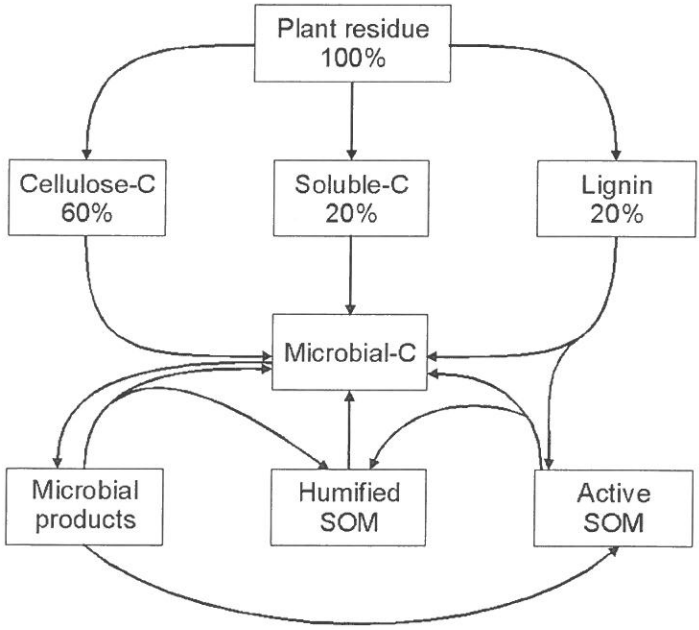

Fig. 3. Plant residue and soil organic matter pools (From Smith *et al.* [72]).

the soil. The composition of humic substances depends on plant vegetation [80]. The active SOM pool consists of readily decomposable C compounds rich in N, P, and S. Microbial biomass pool is central to this model and transforms each component to CO_2, cell biomass and microbial products [72].

The uniqueness of nitrogen consists in the fact that the major N forms in organisms (proteins - including enzymes, nucleic acids and cell wall constituents - chitin and peptidoglycan) are very important for the overall vital activity. Transformations of N in soils include mineralization of organic N, N_2-assimilation, nitrification, denitrification and ammonification. These processes are discussed in the paper "Nitrogen transformations and their circumstances in soil" [82].

PHOSPHORUS AND SULFUR TRANSFORMATION

It is assumed that uptake of P by microorganisms often exceeds that of the higher plants. However, this short-term bacterial immobilization protects some soil P from long-term fixation in soil minerals. Soil microorganisms are involved in the solubilization of insoluble or poorly soluble inorganic forms as well as in the mineralization of organic P. Thus, soil biota facilitates the availability of P to plants and thus takes part in the soil P cycling. Phosphatases, the enzymes involved in P transformation, have been detected on root surfaces, in the rhizosphere soil, and in soil without plant root influence [36,57]. Many plants (for instance clover, soybean, tomato and cereals) are known to exude acid phosphomonoesterases from their roots to soil, especially when the plants are grown in phosphorus deficient nutrient solutions [81]. It has been shown, that fractions of soil organic phosphorus, a product of microbial activity, are transformed rather rapidly in the rhizosphere, where both soil and root phosphatases are active [34]. Figure 4 presents the model of P cycling in nature [57,62].

Sulfur plays a special role in the stabilization of the biologically active structure of proteins. The transformation of sulfur in nature is illustrated in Fig. 5 [57]. Sulphatases are enzymes involved in mineralization of sulphate esters in soil. Elemental sulfur (S^o) must first be converted to sulphate by oxidation before it can be taken up by plants. Nor and Tabatabai [53] detected thiosulphate as one of the intermediates during S^o oxidation. Since rhodanese (thiosulphate sulfurtransferase) converts $S_2O_3^{2-}$ to SO_3^{2-}, they hypothesised that it has a role in S^o oxidation in soil. Deng and Dick [11] suggested that there are other enzyme systems and alternative pathways which are more influential on S^o oxidation than rhodanese.

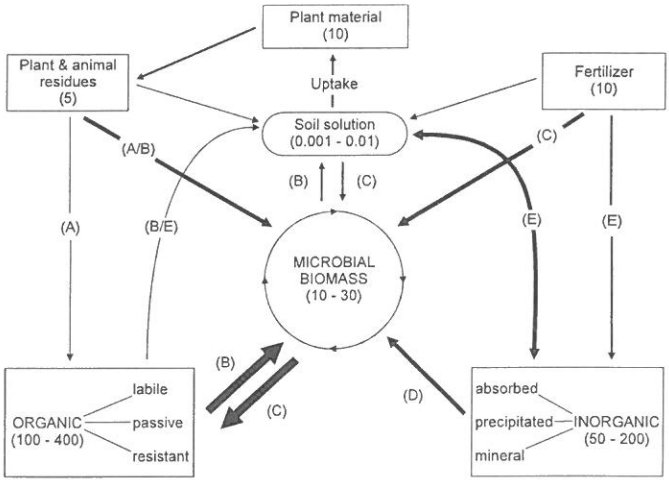

Fig. 4. Schematic representation of phosphorus (P) fractions and flows in soil. The numbers in parentheses indicate amounts of P (kg ha^{-1}, 0-10 cm) in these fractions. A - decomposition; B - mineralization; C - immobilization; D - solubilization; E - inorganic absorption - desorption, precipitation - solubilization (After Paul and Clark [57] from Richardson [62])

IMPORTANCE OF AIR-WATER STATUS FOR BIOCHEMICAL NUTRIENT TRANSFORMATIONS

The soil is naturally exposed to the fluctuation of wet and dry cycles and to diurnal and seasonal temperature gradients. Soil air-water status plays an important role in the regulation of the composition and metabolic activity of soil microorganisms. Waterlogging or flooding the soil creates conditions markedly different from those of a well-drained aerobic soil. In addition to retardation of gaseous exchange between soil and air, waterlogging results in the changes to microbial populations and in series of physico-chemical transformations. Well-aerated soils also include numerous permanently anaerobic aggregates and microhabitats. The existence of microaerophilic and anaerobic microsites in soil is vital to biogeochemical cycling of the nutrients including N, C, P, S, Fe [50,59].

In the absence of molecular oxygen, anaerobic microorganisms (facultative followed by obligatory) utilize oxidised soil components such as NO_3^-, Mn(IV), Fe(III), SO_4^{2-}, CO_2 and dissimilatory products of organic matter as terminal electron acceptors in their respiration [28,31,55,59]. Thus, decomposition of soil organic matter still occurs in O_2 free systems and CO_2 is also formed by anaerobic respiration. Figure 6 illustrates the pathways of soil organic matter decomposition during aerobic and anaerobic respiration [57,61]. The respiration pathways are initiated by action of intracellular dehydrogenases and are terminated (due to the action

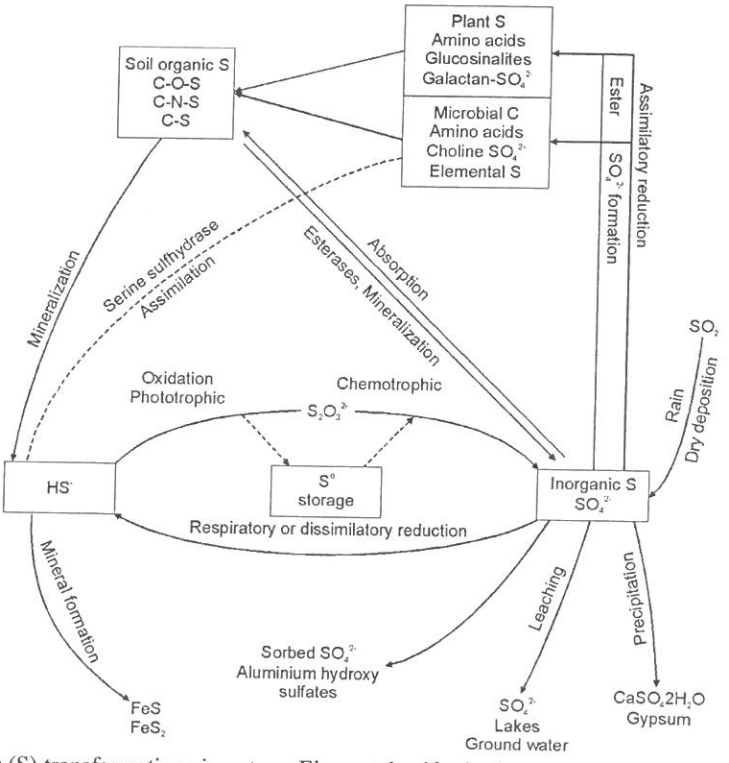

Fig. 5. Sulfur (S) transformations in nature. Elemental sulfur is shown as a storage product, and the possibility of SO_4^{2-} sorption in certain soils is included (From Paul and Clark [57])

of different enzymes, e.g. reductases) in the extracellular medium (soil solution). In the result of anaerobic respiration, the stepwise reduction of soil system takes place, soil redox potential (Eh) decreases, pH alters, and concentrations of reduced N-forms, Mn^{2+}, Fe^{2+}, S^{2-} and CH_4 increase [24,25,31,55].

It has been observed that dehydrogenase activity is higher in flooded than in well-aerated soil [4,79], and an increase of this activity is accompanied by a decrease of redox potential [54,58]. Studies of soil in its natural sites, as well as under controlled air-water conditions, showed the close relationship between soil dehydrogenase activity and aeration status [5,6,26,27,28,29,74,75,76,77]. This fact results probably from the much more energetic efficiency of an aerobic respiration (with utilization O_2 as terminal electron acceptor) than that of an anaerobic one. It has been shown that dehydrogenase activity varied during preincubation of the soil under different aeration conditions and was negatively correlated with air-filled porosity (Eg), oxygen diffusion rate (ODR) and redox potential, but positively with water content and concentration of reduced Fe [74,76]. Brzezińska *et al.* [5]

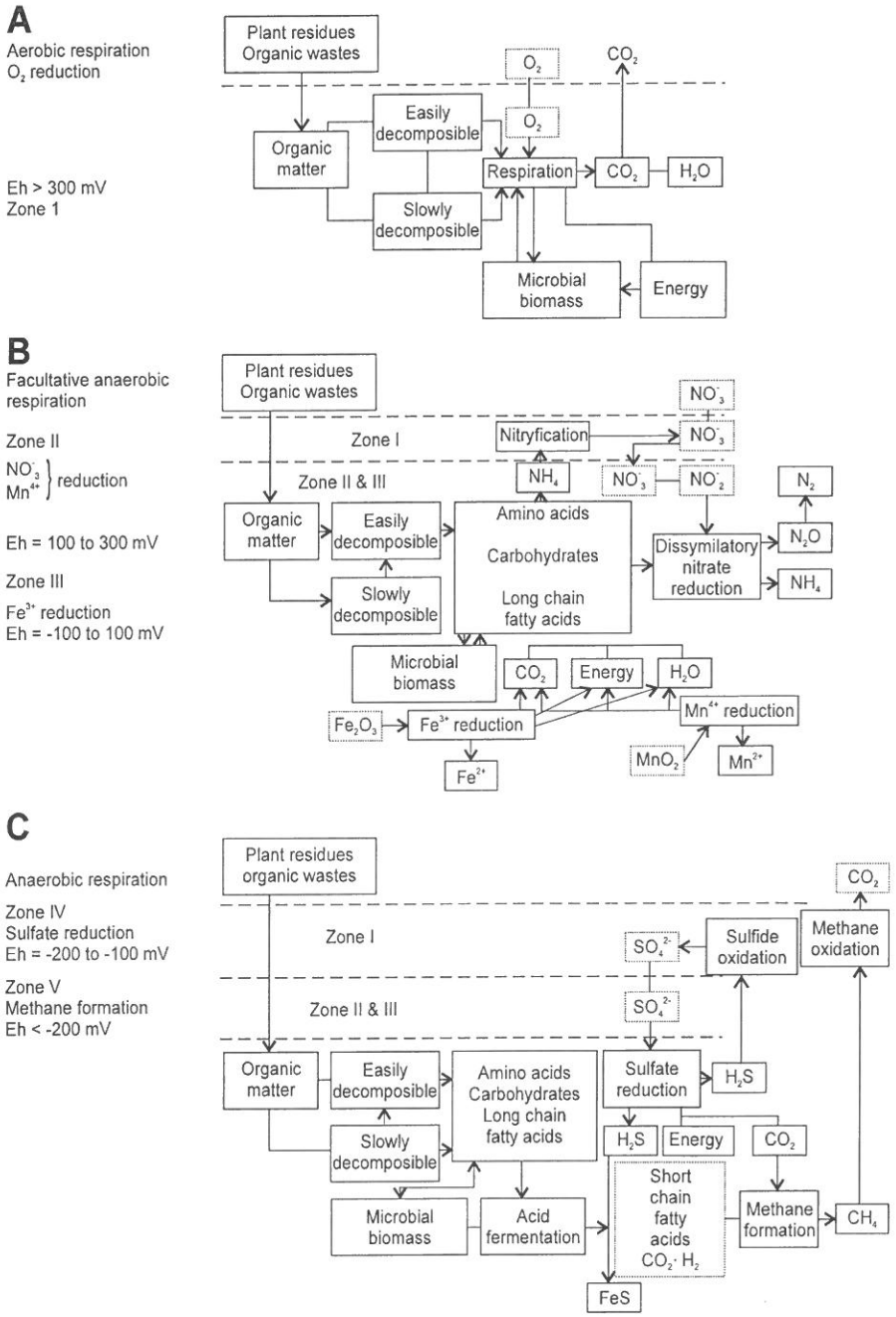

Fig. 6. Pathways of organic matter decomposition during aerobic respiration (A), facultative anaerobic respiration (B), and anaerobic respiration (C) (From Reddy *et al.* [61]).

observed that the modification of the soil physical properties such as water content and temperature, caused up to 150-fold of the dehydrogenase activity value of loess soils. They showed that the electron activity of the soil solution (reflected by Eh) is more important for the activity of soil dehydrogenases than the direct availability of O_2 (measured by ODR). Figures 7-9 show the relations between dehydrogenase activity and aeration parameters such as Eg, ODR and Eh [5,74,76].

Studies of catalase activity showed its dependence on soil aeration status expressed as ODR and Eh [26,27,74]. Figure 10 shows the relation between soil catalase activity and soil aeration status expressed as D/Do [74].

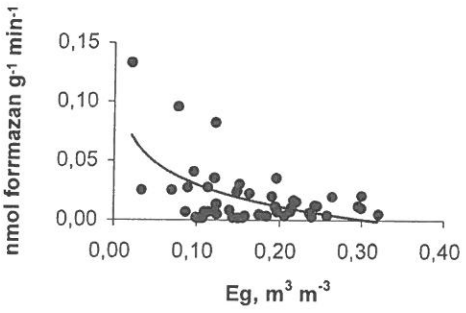

Fig. 7. Relationship between soil dehydrogenase activity and air-filled porosity (Eg) under controlled soil aeration status (From Stępniewska *et al.* [74]).

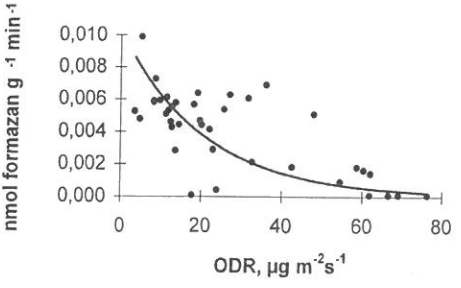

Fig. 8. Relation between soil dehydrogenase activity and oxygen diffusion rate (ODR) after preincubation under different air-water conditions (From Stępniewski *et al.* [76]).

Pulford and Tabatabai [59] studied the effect of redox potential on the activity of eight enzymes involved in C, N, P and S cycling on soil. They observed that the hydrolysis of native soil organic P and pyrophosphate added to soil is significantly affected by waterlogging. Mostly decreases in phosphatase activities were found, especially in acid and alkaline phosphatase and pyrophosphatase activities. Some soils showed the increase in phosphodiesterase activity. The activity of arylsulphatase diminished and the change in activity of β-glucosidase depended on the soil. Urease activity decreased but amidase activities increased after soil waterlogging. The increase in enzyme activities was perhaps due to inhibition by the reduced metal ions produced upon soil flooding. The increase of enzyme activity resulted probably from the activation of these enzymes by the released metal ions or an increase in the concentration of the enzymes due to microbial adaptation to the reduced environment [59].

Well aerated soils always have a marked ligninolytic activity with an appropriate microflora and it is possible that this microflora is also active in the degradation of

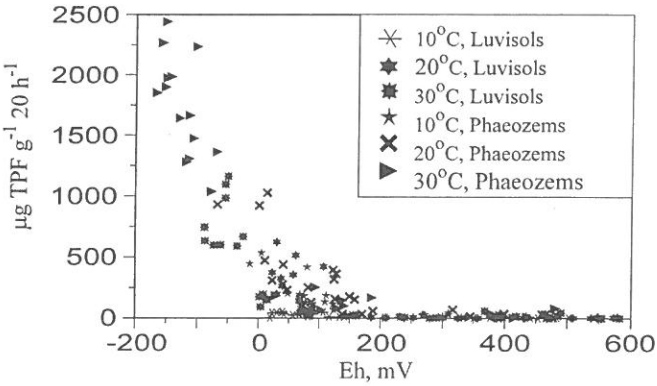

Fig. 9. Relationship between soil dehydrogenase activity and redox potential (Eh) in soils conditioned under controlled temperature and aeration conditions (From Brzezińska *et al.* [5])

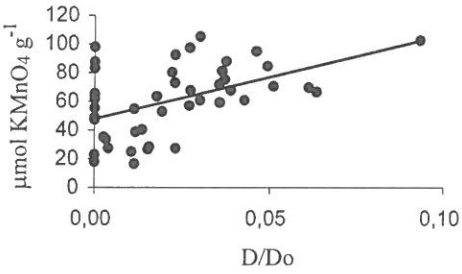

Fig. 10. Relation between catalase activity and gas diffusion coefficient (D/Do) (From Stępniewska *et al.* [74])

humic compounds, once their intimate association with an inorganic or a structural matrix has been disturbed [33,48].

Deng and Dick [11] reported a change of rhodanese activity with decreasing water potential. Ray *et al.* [60] showed a 2.5 - to 6 - fold increase in rhodanese activity in a pokkali (acid sulphate) soil after flooding but no changes when an alluvial was flooded.

Although invertase and amylase activities in seven studied soils were found to be uncorrelated with soil moisture content [64], some differences in the magnitude of the ratio of invertase to amylase activity among groups of soils in tussock grassland were partly explained by variations in soil moisture [65].

In the paper an attempt has been made to present a general description of this broad and complex topic. Soil is an extremely heterogeneous environmental system in which different physical phases (e.g., solid, liquid, and gaseous) and numerous biotic (e.g., microorganisms, small animals, plant roots, enzymes) and abiotic (e.g., clay minerals, humus material, organomineral aggregates) components are involved in physical, chemical and biological processes. Enzymes ensure the movement of materials among the biotic and abiotic portions of soil environment - all biochemical transformations in soil are dependent on, or related to the presence of enzymes [23].

REFERENCES

1. **Alef K., Nannipieri P.:** Enzyme activities. In: Methods in Applied Soil Microbiology and Biochemistry (Eds K. Alef, P. Nannipieri). Acad. Press, Harcourt Brace & Company Publishers, London, 311-373, 1995.
2. **Alef K., Nannipieri P., Traza-Cepeda C.:** Phosphatase activity. In: Methods in Applied Soil Microbiology and Biochemistry (Eds K. Alef, P. Nannipieri). Acad. Press, Harcourt Brace & Company, Publishers, London, 335-344, 1995.
3. **Bandick A.K., Dick R.P.:** Field management effects on soil enzyme activities. Soil Biol. Biochem., 31, 1471-1479, 1999.
4. **Baruah M., Mishra R. R.:** Dehydrogenase and urease activities in ricefield soils. Soil Biol. & Biochem., 16, 423-424, 1984.
5. **Brzezińska M., Stępniewska M., Stępniewski W.:** Soil oxygen status and dehydrogenase activity. Soil Biol. Biochem., 30, 1783-1790, 1998.
6. **Brzezińska M., Stępniewska Z., Stępniewski W., Włodarczyk T., Przywara G., Bennicelli R.:** Effect of oxygen deficiency on soil dehydrogenase activity (pot experiment with barley). Int. Agrophysics, 15, 3-7, 2001.
7. **Burns R.G.:** Enzyme activity in soils: some theoretical and practical considerations. In: Soil Enzymes (Ed R.G. Burns). Acad. Press, London, 8, 295-326, 1978.
8. **Burns R.G.:** Enzyme activity in soil: Location and possible role in microbial ecology. Soil Biol. Biochem., 14, 423-427, 1982.
9. **Clark A.E., Stone B.A.:** Properties of a -1,4-glucan hydrolase from *Aspergillus niger*. Biochem. J., 96, 802-807, 1965.
10. **Curl E.A., Harper J.D.** Fauna-microflora interactions. In: The Rhizosphere (Ed. J.M. Lynch). Wiley-Interscience, New York, 369-388, 1990.
11. **Deng S., Dick R.P.:** Sulfur oxidation and rhodanese activity in soils. Soil Sci., 150, 552-560, 1990.
12. **Deng S.P., Tabatabai M.A.:** Effect of tillage and residue management on enzyme activities in soils. I. Amidohydrolases. Biol. Fert. Soils, 22, 202-207, 1996.
13. **Dick W.A., Tabatabai M.A.:** Significance and potential uses of soil enzymes. In: Soil Microbial Ecology (Ed. F.B.Jr Metting). Marcel Dekker, Inc., New York, Basel, Hong Kong, 4, 95-127, 1993.
14. **Dilly O., Nannipieri P.:** Intracellular and extracellular enzyme activity in soil with reference to elemental cycling. Z. Pflanzen. Bodenkd., 161, 243-248, 1998.
15. **Eriksson K.E., Wood T.M.:** Biodegradation of cellulose. In: Biosynthesis and biodegradation of wood components (Ed. T. Higuchi). Acad. Press, New York, 469-503, 1985.
16. **Falih A.M.K., Wainwright M.:** Microbial and enzyme activity in soils ameneded with a natural source of easily available carbon. Biol. Fertil. Soils, 21, 177-183, 1996.
17. **Foster R.C., Rovira A.D., Cock T.W.:** Ultrastructure of the root-soil interface. American Phytopatological Society, St. Paul, MN, 1983.
18. **Frankenberger W.T.Jr., Dick W.A.:** Relationships between enzyme activities and microbial growth and activity indices in soil. Soil Sci. Soc. Am. J., 47, 945-951, 1983.
19. **Frankenberger W.T.Jr, Tabatabai M.A.:** Factors affecting L-asparaginase activity in soils. Biol. Fertil. Soils, 11, 1-5-, 1991.
20. **Frankenberger W.T.Jr., Tabatabai M.A.:** L-Glutaminase activity if soils. Soil Biol. Biochem., 23, 869-874, 1991.
21. **Frankenberger W.T.Jr., Tabatabai M.A.:** Enzyme activity of soils. In: Methods in Applied Soil Microbiology and Biochemistry (Eds K. Alef, P. Nannipieri). Acad. Press, Harcourt Brace & Company Publishers, London, 321 -330, 1995.

22. **Galstian A.Sh.:** Enzymatic activity of soils. Geoderma, 12, 43-48, 1974.
23. **Gianfreda L., Bollag J.M.:** Influence of natural and anthropogenic factors on enzyme activity in soil. In: Soil Biochemistry (Eds G. Stocky, J.M. Bollag). Marcel Dekker Inc, New York, Basel, Hong Kong,, 9(4), 122-193, 1996.
24. **Gliński J., Stahr K., Stępniewska Z., Brzezińska M.:** Changes of redox and pH conditions in a flooded soil amended with glucose and nitrate under laboratory conditions. Z. Pflanzen. Bodenk., 155, 13-17, 1991.
25. **Gliński J., Stahr K., Stępniewska Z., Brzezińska M.:** Changes of redox and pH conditions in a flooded soil amended with glucose and manganese oxide under laboratory conditions. Z. Pflanzen. Bodenk., 159, 297-304, 1996.
26. **Gliński J., Stępniewska Z., Brzezińska M.:** Characterization of the dehydrogenase and catalase activity of the soils of two natural sites with respect to the soil oxygenation status. Pol. J. Soil Sci., 19, 47-52, 1986.
27. **Gliński J., Stępniewska Z., Kasiak A.:** Changes of soil enzyme activity at different water and oxygen content (in Polish). Roczn. Glebozn., 34, 53-59, 1983.
28. **Gliński J., Stępniewski W.:** Soil Aeration and its Role for Plants. CRC Press, Boca Raton, Florida, 1985.
29. **Gliński J., Stępniewski W., Stępniewska Z., Włodarczyk T., Brzezińska M.:** Characteristics of aeration properties of selected soil profiles from Central Europe. Int. Agrophysics, 14, 17-31, 2000.
30. **Gostkowska K., Furczak J.:** The effect of the cultivation system used on the microbiological activity of loess soil. Pol. J. Soil Sci., 16, 1, 39-45, 1983.
31. **Gunnison D., Engler R. M., Patrick W.H.Jr.:** Chemistry and microbiology of newly flooded soils: relationship to reservoir - water quality. In: Microbial Processes in Reservoirs (Ed. D. Gunnison). Dr W. Junk Publishers, Dordrecht, Boston, Lancaster, 39-57, 1985.
32. **Guwy A.J., Martin S.R., Hawkes F.R., Hawkes D.L.:** Catalase activity measurements in suspended aerobic biomass and soil samples. Enz. Microb. Techn., 25, 669-676, 1999.
33. **Haider K.:** Problems related to the humification process in soils of temperate climates. In: Soil Biochemistry 7 (Eds G. Stocky, J.M. Bollag). Marcel Dekker Inc, New York, Basel, Hong Kong, 7(2), 55-94, 1992.
34. **Helal H.M., Sauerbeck D.:** Soil and root phosphatase activity and the utilization of inositol phosphates as dependent on phosphorus supply. In: Plant Roots and their Environment (Eds B.L. McMichael, H. Persson). Elsevier Sci. Publ., B.V., 1991.
35. **Jenkinson D.S.:** The fate of plant and animal residues in soil. In: The Chemistry of Soil Processes (Eds D.J. Greenland, M.H.B Hayes). John Wiley & Sons, New York, 506-561, 1981.
36. **Joner E.J., Magid J., Gahoonia T.S., Jakobsen I.:** P depletion and activity of phosphatases in the rhizosphere of mycorrhizal and non-mycorrhizal cucumber (*Cucumis sativus L.*). Soil Biol. Biochem., 327, 1145-1151, 1995.
37. **Kandeler E., Tscherko D., Spiegel H.:** Long-term monitoring of microbial biomass, N mineralization and enzyme activities of a Chernozem under different tillage management. Biol. Fert. Soils, 28, 343-351, 1999.
38. **Kirk T.K., Farrell L.:** Enzymatic "combustion: the microbial degradation of lignin. Annu. Rev. Microbiol. 41, 465-505, 1987.
39. **Kirk T.K., Shimada M.:** Lignin biodegradation: the microorganisms involved, and the physiology and biochemistry of degradation by white-rot fungi. In: Biosynthesis and Biodegradation of Wood Components (Ed. T. Higuchi). Acad. Press, New York, 579-605, 1985.
40. **Kiss S., Dragan-Bularda M., Radulescu D.:** Biological significance of enzymes accumulated in soil. Adv. Agron., 27, 25-87, 1975.
41. **Kobus J., Kurek E., Józefaciuk C.:** The influence of organic fertilization on the biological activity of degraded loess soil. Roczn. Gleb., 39, 4, 159-170, 1988.

42. **Kotełko K., Sedlaczek L., Lachowicz T.M.:** Biology of Bacteria (In Polish). PWN Wrocław, 2, 94-271, 1979.
43. **Kucharski J., Niklewska T.:** The effect of manuring with straw on microbial properties of light soil (In Polish). Pol. J. Soil Sci., 24, 2, 171-177, 1991.
44. **Kuprevich V.F., Shcherbakova T.A.:** Comparative enzymatic activity in diverse types of soil. In: Soil Biochemistry (Eds A.D. McLaren, J. Skujins). Marcel Dekker Inc, New York, 2, 167-201, 1971.
45. **Ladd J.N.:** Origin and range of enzymes in soil. In: Soil Enzymes (Ed. R.G. Burns). Acad. Press, London, 2, 51-96, 1978.
46. **Ladd J.N., Foster R.C., Nannipieri P., Oades J.M.:** Soil structure and biological activity. In: Soil Biochemistry (Eds G. Stocky, J.M. Bollag). Marcel Dekker Inc, New York, Basel, Hong Kong, 9(2), 23-78, 1996.
47. **Loll M.J., Bollag J.M.:** Protein transformation in soil. Adv. Agron., 36, 351-382, 1983.
48. **Martin J.P., Haider K. Kassim G.:** Biodegradation and stabilization after 2 years of specific crop, lignin, and polysaccharide carbons in soils. Soil Sci. Soc. Am. J., 44, 1250-1255, 1980.
49. **Megharaj M., Singleton I., Kookana R., Naidu R.:** Persistence and effects of fenamiphos on native algal populations and enzymatic activities in soil. Soil Biol. Biochem., 31,1549-1553, 1999.
50. **Metting F.B.Jr.:** Structure and physiological ecology of soil microbial communities. In: Soil Microbial Ecology (Ed. Metting F.B.Jr.) Marcel Dekker, Inc., New York, Basel, Hong Kong, 1, 3-25, 1993.
51. **Myśków W., Stachyra A., Zięba S., Masiak D.:** Biological activity as index of soil fertility (In Polish). Roczn. Gleb., 47, 1/2, 88-99, 1996.
52. **Nannipieri P., Grego S., Ceccanti B.:** Ecological significance of the biological activity in soil. In: Soil Biochemistry (Eds J.M. Bollag, G. Stocky). Marcel Dekker Inc, New York, Basel, Hong Kong, 6(6), 293-355, 1990.
53. **Nor Y.M., Tabatabai M.A.:** Colorimetric determination of microgram quantities of thiosulfate and tetrathionate. Anal. Lett., 8, 537-547, 1975.
54. **Okazaki M., Hirata E., Tensho K.:** TTC reduction in submerged soils. Soil Sci. Plant Nutr., 29, 489-497, 1983.
55. **Ottow J.C.G.:** Bedeutung des Redoxpotentials für die Reduktion von Nitrat und Fe(III)-Oxiden in Böden. Z. Pflanzen. Bodenkd., 145, 91-93, 1982.
56. **Paul E.A.:** Dynamics of organic matter in soils. Plant Soil, 76, 275-285, 1976.
57. **Paul E.A., Clark F.E.:** Soil Microbiology and Biochemistry (Eds E.A. Paul, F.E. Clark). Acad. Press, Inc., 129-179, and 289-313, 1996.
58. **Pedrazzini F.R., McKee K.L.:** Effect of flooding on activities of soil dehydrogenases in rice (*Oryza sativa L.*) roots. Soil Sci. Plant Nutr., 30, 359-366, 1984.
59. **Pulford I.D., Tabatabai M.A.:** Effect of waterlogging on enzyme activities on soils. Soil Biol. Biochem., 20, 215-219, 1988.
60. **Ray R.C., Beherea N., Sethunathan N.:** Rhodanese activity of flooded and nonflooded soils. Soil Biol. Biochem. 17, 159, 162, 1985.
61. **Reddy K.R., Feijtel T.C., Patrick W.H.:** Effect of soil redox conditions on microbial oxidation of organic matter. In: The Role of Organic Matter in Modern Agriculture (Eds Y. Chen, Y. Avnimelech). Nijhoff, Dordrecht, 117-153, 1986.
62. **Richardson A.E.:** Soil microorganisms and phosphorus availability. In: Soil Biota (Eds C.E. Pankhurst, B.M, Doube). CSIRO, East Melbourne, 1994.
63. **Ross D.J.:** A seasonal study of oxygen uptake of some pasture soils and activities of enzymes hydrolysing sucrose and starch. J. Soil Sci., 16, 73-85, 1965.
64. **Ross D.J.:** Some enzyme and respiratory activities of tropical soils from New Herbides. Soil Biol. Biochem., 5, 559-567, 1973.

65. **Ross D.J.:** Studies on a climosequence of soils in tussock grasslands. Invertase and amylase activities of topsoils and their relationship with other properties. New Zeal. J. Sci., 18, 511-518, 1975.
66. **Ruggiero P., Dec J., Bollag J.M.:** Soil as a catalytic system. In: Soil Biochemistry, Vol. 9. (Eds G. Stocky, J.M. Bollag). Marcel Dekker Inc, New York, Basel, Hong Kong, Chapter 3, 79-122, 1996.
67. **Schäffer A.:** Pesticide effects on enzyme activities in the soil ecosystem. In: Soil Biochemistry, Vol. 8. (Eds J.M. Bollag, G. Stocky). Marcel Dekker Inc, New York, Basel, Hong Kong, Chapter 8, 273-340.
68. **Schinner F., von Mersi W.:** Xylanase-, cellulase- and invertase activity in soil: an improved method. Soil Biol. Biochem. 22, 511, 515, 1990.
69. **Schoemaker H.E., Harvey P.J., Bowen R.M., Palmer J.M.:** On the mechanism of enzymatic lignin break-down. Fed. Eur. Biochem. Soc., 183, 7-12, 1985.
70. **Skujins J.:** Extracellular enzymes in soil. CRC Crit. Rev. Microbiol., 4, 383-421, 1976.
71. **Skujins J.:** History of abiontic soil enzymes research In: Soil Enzymes (Ed R.G. Burns). Acad. Press, London, 1, 1-49, 1978.
72. **Smith J.L., Papendick R.I., Bezdicek D.F., Lynch J.M.:** Soil organic matter dynamics and crop residue management. In: Soil Microbial Ecology (Ed. F.B.Jr. Metting). Marcel Dekker, Inc., New York, Basel, Hong Kong, 3, 65-94, 1993.
73. **Stevenson F.J.:** Cycles of soil: carbon, nitrogen, phosphorus, sulphur, micronutrients. John Wiley & Sons, New York, 1986.
74. **Stępniewska Z., Brzezińska M., Gliński J., Stępniewski W., Włodarczyk T., Čurlik J., Houšková B.:** Aeration status of some Slovakian soils. Int. Agrophysics, 14, 327-339, 2000.
75. **Stępniewska Z., Gliński J., Włodarczyk T., Brzezińska M., Blum W.E.H., Rampazzo N., Wimmer B.:** Soil aeration status of some Austrian soils. Int. Agrophysics, 11, 199-206, 1997.
76. **Stępniewski W., Stępniewska Z., Gliński J., Brzezińska M., Włodarczyk T., Przywara G., Várallayay G., Rajkai K.:** Dehydrogenase activity of some Hungarian soils as related to their water and aeration status. Int. Agrophysics, 14, 341-354, 2000.
77. **Stępniewski W., Stępniewska Z., Włodarczyk T., Dąbek-Szreniawska M., Brzezińska M., Słowińska-Jurkiewicz A., Przywara G.:** Aeration related properties and their influence on soil biological parameters. Int. Agrophysics, 7, 163-173, 1993.
78. **Stott D.E., Kassim G., Jarrel W.M., Martin J.P., Haider K.:** Stabilization and incorporation into biomass of specific plant carbon during biodegradation in soil. Plant Soil, 70, 15-26, 1983.
79. **Tiwari M. B., Tiwari B. K., Mishra R. R.:** Enzyme activity and carbon dioxide evolution from upland and wetland rice soils under three agricultural practices in hilly regions. Biol. Fertil. Soils, 7, 359-364, 1989.
80. **Turski R., Flis-Bujak M.:** The influence of crop rotation on the composition of humic compounds in loess soils. Pam. Puł., 77, 33-47, 1982.
81. **Vuorinen A.H., Saharinen M.H.:** Effects of soil organic matter extracted from soil on acid phosphomonoesterase. Soil Biol. Biochem., 10/11, 1477-1481, 1996.
82. **Włodarczyk T.:** Nitrogen transformations and their circumstances in soils. Acta Agrophysica 61, 2002.

ZNACZENIE ENZYMÓW GLEBOWYCH W PRZEKSZTAŁCANIU SKŁADNIKÓW POKARMOWYCH

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S t r e s z c z e n i e: Gleba jest środowiskiem, w którym zachodzą różnorodne procesy biotyczne i abiotyczne. Dynamiczny charakter oraz złożona budowa chemiczna glebowej materii organicznej powodują, że jest ona ważnym źródłem składników pokarmowych niezbędnych do rozwoju roślin. Uruchamianie oraz obieg substancji pokarmowych w środowisku glebowym zachodzą w znacznym stopniu w wyniku katalizy enzymatycznej. Praca zawiera podstawowe informacje dotyczące źródła enzymów glebowych, ich lokalizacji w glebie oraz roli w transformacji składników pokarmowych. Podkreślono znaczenie warunków wodno-powietrznych gleby dla funkcjonowania enzymów glebowych.

S ł o w a k l u c z o w e: gleba, aktywność enzymatyczna, obieg składników pokarmowych.