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SOIL AERATION STATUS AND CATALASE ACTIVITY

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Abstract. Soil catalase activity was determined as a function of soil aeration status of an Orthic Luvisol in a pot experiment. Soil was compacted to 1.2, 1.35 or 1.5 Mg m^{-3} bulk density and water content was maintained in the readily available range for plants (pF 2.2-2.9). Three levels of soil hypoxia were applied by raising soil water content to pF 1.3-1.7 and pF 0 (flooding). Soil aeration properties (air filled porosity – Eg; oxygen diffusion rate – ODR, redox potential – Eh; content of reduced iron [Fe^{+2}]), as influenced by combined effects of water potential and compaction level, showed significant interrelationships. Soil catalase activity was found to be depressed under hypoxic conditions by an average of 16% only. Among the properties tested, ODR and Eh best described the relationship between soil oxygen status and catalase activity.

Keywords: soil aeration, catalase activity, soil hypoxia

INTRODUCTION

Catalase (EC 1.11.1.6) is a heme-containing enzyme that catalyses decomposition of H_2O_2 to water and molecular oxygen. Hydrogen peroxide and other reactive oxygen species, formed during aerobic respiration as a by-product in a number of cellular systems, are the price aerobic organisms pay for the high efficiency of O_2-dependent respiration metabolism. Because of its extreme reactivity, H_2O_2 creates a risk of irreversible damage to proteins by oxidising the SH-groups [1,11]. Catalase, along with peroxidases and superoxide dismutase, serves as an efficient scavenger of reactive oxygen species.

Soil catalase activity shows a significant correlation with organic carbon content, soil microbial biomass, O_2 consumption, CO_2 evolution, and dehydrogenase, amidase, glucosidase and esterase activity [3,6,7,15,19].

Metabolism of soil biota is strongly influenced by soil physical status. Soil compaction reduces the total soil pore volume and changes pore size distribution. Replacement of the gas phase by water after soil flooding causes a rapid exhaustion of oxygen. This results in a shift in soil microbial populations from aerobic to anaerobic microorganisms. Catalases are synthesized by all aerobes and most of the facultative anaerobes, but not by obligate anaerobes [1,28]. Changes in catalase activity in soils with changing soil aeration, have been observed in model experiments as well as under natural field conditions [8,10,23,24].

The objective of the present study was to determine the effect of important physical factors such as soil water content and compaction on soil aeration status and catalase activity in a greenhouse pot-experiment with triticale vegetation grown on an Orthic Luvisol.

MATERIAL AND METHODS

The soil material used was the Ap horizon of an Ortic Luvisol developed from loess (25% sand, 70% silt, 5% clay, 1.54% organic C, 6.5 pH_{H_2O}). The experimental site is located in the south-east part of Poland where soils developed from loess dominate. Under Polish conditions, flooding usually occurs in the river valleys constituting about 5% of the territory, but saturation with water can occur in other soils during spring snow melting and under the conditions of prolonged rainfalls.

Soil was sieved without drying through a 5 mm sieve. Plastic pots (6 dm^3 in volume, 20 cm in height) were filled with the soil at three compaction levels prepared manually: 1.20, 1.35 and 1.50 Mg m^{-3}. Before sowing, the soil was fertilized with 0.1 g N, 0.125 g K and 0.066 g P kg dry $soil^{-1}$ in the form of NH_4NO_3, K_2SO_4 and KCl, and $CaHPO_4 \cdot 2H2O$, respectively. After three days of soil conditioning, seeds of triticale (cv. "Jago") were sown at 2 cm depth into the soil. The seedlings were thinned after the emergence to 25 plants per pot. The experiment was conducted in a greenhouse during the vegetation season. Triticale (used primarily for livestock feed) is the stabilized hybrid of wheat (*Triticum*) and rye (*Secale*).

Soil water status was maintained at the control level in the readily available range for plants, corresponding to pF 2.2-2.9, except during the three stress periods. During the stress periods, the soil water content was elevated from the control level to the water potential of pF 1.3-1.7, or to pF 0 with a 5-10 mm water layer on the soil surface, at each bulk density.

Four replicate pots for each combination of compaction and water content level were prepared. The 14-day oxygen deficiency stresses were applied at three plant physiological stages: at tillering (stress I); at shooting (stress II); and at the beginning of flowering (stress III). A complete set of 36 pots was prepared for each successive stress (nine combinations x four replications); the experiment comprised a total of 108 pots.

Measurements were made four times during each stress period. Before soil sampling, oxygen diffusion rate (*ODR*) and redox potential (*Eh*) were measured at 2 cm soil depth vs. saturated calomel electrode [9,18].

Soil water content was determined gravimetrically (105°C). To compare the air-water status in the experimental treatments, calculations were made as follows: volumetric water content = (gravimetric water content) x (bulk density); total porosity = (1 – bulk density/particle density)100; air-filled porosity = total porosity – volu-metric water content [4,9].

Soil was sampled (0-5 cm) at three locations in each pot and thoroughly mixed together (all visible roots were removed). Determination of reduced iron content, [Fe^{+2}] was made in 0.05 M sulphuric acid extracts with the use of α,α'-dipyridyl in acetate buffer at pH 4.5 [2]. Catalase activity was determined according to Johnson and Temple [14]. To eliminate probable overestimation of enzyme activity due to chemical reduction of added H_2O_2, a correction for autoclaved soil (0.1 MPa, 120°C, 30 min) was made. The residual H_2O_2 was determined by titration with 0.02 M $KMnO_4$ in the presence of H_2SO_4. The results were expressed in μmol H_2O_2 consumed g^{-1} min^{-1}. The content of Fe^{+2} and the enzyme activity were calculated on the basis of the oven-dry soil weight (105°C).

The data was subjected to variance analysis (Statgraphics 5.0) using the least significant difference test and comparing the differences among the treatments.

RESULTS AND DISCUSSION

In the study we focused on the response of soil catalases to changes in soil aeration status. The aeration status in loose soil held in the readily available range of water for plants (pF 2.2-2.9) was established as the control aeration level. Changes in soil aeration were obtained by manipulation of soil bulk density and water content.

Effect of Soil Water Potential and Compaction on Soil Aeration Parameters

The average percentages of solid, liquid and gaseous phases in the soil volume under the experimental conditions are presented in Table 1. Soil compaction influences the course of the pF-soil moisture characteristics. Besides, because macropore continuity is of major importance to the aeration status of the soil, the effect of soil compaction on other aeration properties depended on soil hydro-physical status [17,29,30]. Values presented in Figure 1 characterize the aeration properties of the Orthic Luvisol averaged for nine experimental treatments. Soil compaction significantly affected the values of oxygen diffusion ($P<0.001$) and redox potential ($P<0.01$), but not significantly the content of reduced Fe. The influence of soil density

on *ODR* rate was observed in different soil systems [13,26]. In the tested loess soil, larger changes in oxygen availability were observed at pF 1.3-1.7 (*ODR* decreased from 44.8 μg $m^{-2}s^{-1}$ to 19.6 μg $m^{-2}s^{-1}$) than in drier soil at pF >2.2 (*ODR* decreased from 82.4 μg $m^{-2}s^{-1}$ to 50.2 μg $m^{-2}s^{-1}$) (Fig. 1a).

Table 1. Comparison of the distribution of soil physical phases in Orthic Luvisol experimental treatments (averages for entire experiment)

Bulk density	Solid phase	Total porosity	Water-filled porosity* (%, v/v) at pF			Air-filled porosity (%, v/v) at pF		
Mg m^{-3}	(%, v/v)	(%, v/v)	2.2-2.9	1.3-1.7	0	2.2-2.9	1.3-1.7	0
1.20	46.5	53.5	19.9	30.1	47.9	33.6	23.4	5.50
1.35	52.3	47.7	24.5	33.2	47.3	23.2	14.5	0.40
1.50	58.1	41.9	27.9	35.8	42.2	14.0	6.1	0.01

*Water-filled porosity = volumetric water content

The effect of soil compaction on redox potential was greater than that for *ODR*, at moderate water potential, resulting in lowering of *Eh* by 77 mV and 96 mV in the two denser treatments, as compared to the most loose soil treatment. At the control water level (>pF 2.2) *Eh* diminished slightly (<50 mV), but under flooding *Eh* values were close to 166 mV in all the compaction treatments (Fig. 1b). The content of Fe^{+2} did not change significantly with compaction.

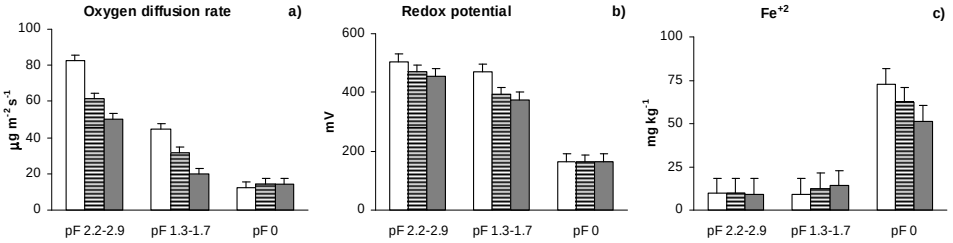

Fig. 1. Average values of soil aeration properties (*ODR*, *Eh* and Fe^{+2}) in an Orthic Luvisol for combinations of soil densities (1.20, 1.35 and 1.50 Mg m^{-3}) and water potentials (pF 2.2-2.9, pF 1.3-1.7 and pF 0)

Modification of soil water status significantly differentiated all aeration properties ($P<0.001$). As compared to the control water potential, the value of *Eg* decreased up to 20 times, *ODR* decreased up to 7 times, *Eh* decreased even by 340 mV, whereas Fe^{+2} content increased up to 8 times.

It is interesting that *ODR* changed gradually for particular water potential treatments (Fig. 1a), but *Eh* and, especially, [Fe^{+2}] changed sharply only under flooding (Fig. 1b-c). Despite the restriction of O_2 diffusion at pF 1.3-1.7 (as compared to the aerated control >pF 2.2), the redox potential remained on a relatively

high level, i.e., about 400 mV. Simultaneously, the content of reduced Fe at pF 1.3-1.7 was comparable to that observed in the control soil. This resistance against soil reduction could possibly result from the presence of NO_3^-, derived from fertilizers, because, generally, under oxygen deficiency, Fe is reduced only after NO_3^- exhaustion [9]. The *Eh* value proximal to 400 mV confirmed this hypothesis. Without NO_3^- amendments, the tested soil showed high susceptibility to redox transformations with t_{300}<0.2 day (results not shown). The t_{400} and t_{300} indexes represented the period of time needed to lower the *Eh* value in submerged soil (under defined conditions) to 400 mV (corresponding to NO_3^- reduction) and 300 mV (corresponding to Fe^{+3} reduction), respectively [24], and indicated that NO_3^- and Fe reduction were important components of soil redox buffering capacity.

Effect of Water Potential and Compaction on Soil Catalase Activity

Soil compaction reduces the total soil pore volume and changes the pore size distribution (towards a higher percentage of small pores) as well as increases tortuosity of soil pores [25,29]. Under water excess, restricted gas exchange leads to anaerobiosis with a number of consequences (shift in microbial populations, change in respiration metabolism, decrease in soil redox potential, pH change, etc.). Thus, any modification of soil water content and bulk density (both naturally and due to soil management system) indirectly changes the composition, behaviour and function of soil micro-organisms.

Catalase activity of Orthic Luvisol ranged from 3.81 to 10.2 μMol H_2O_2 g^{-1} min^{-1} and followed the changes in soil aeration properties. The level of catalase activity at the control water potential (>pF 2.2) was the highest at a density of 1.2 Mg m^{-3} (average 7.20 μMol H_2O_2 g^{-1} min^{-1}), and decreased under poor aeration (i.e., in more compacted and wetter soils, Fig. 2). The soil density factor was found to be insignificant for catalase activity.

Soil moisture significantly affected soil catalase activity (P<0.001). Catalase activity was inhibited in the least dense soil by 8% (at pF 1.3-1.7), and by 15% under flooding; in denser soil the decrease was 4% and 11%, whereas in most compacted the changes were 7% and 11%, respectively. Assuming that average catalase activity expressed by the aerated treatment (control moisture in the least compact soil) reached its maximal level (100%), a 16% depression under hypoxia (flooding of the most compact soil) was observed.

The average catalase activities observed for the three oxygen deficiency stresses (applied at the stage of tillering, at the next shooting, and at the start of flowering) were 6.52, 6.55 and 6.52 μMol H_2O_2 g^{-1} min^{-1}, respectively. Thus, the phase of plant vegetation did not influence soil catalase activity and it may be hypothesized that catalase activity was generated by microbial cells, with no significant contribution from plant roots.

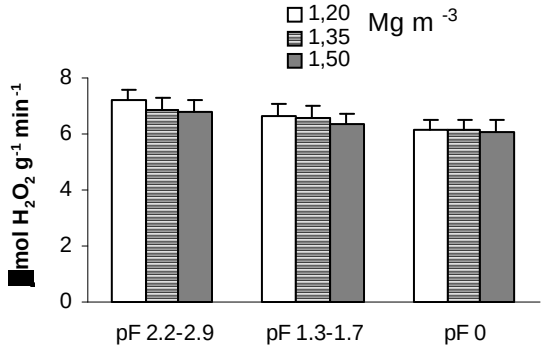

Fig. 2. Combined effect of soil compaction and water potential on soil catalase activity in the Orthic Luvisol (average values)

Relationships among the aeration parameters

Soil aeration properties were significantly interrelated (Tab. 2). Examples of these relations are shown in Figure 3.

Table 2. Relationships observed in the Orthic Luvisol under conditions of different soil aeration status (correlation coefficients of linear equations)

Aeration parameter	ODR	Eh	Fe^{+2}	CAT
Water content (%, v/v)	-0.733^{***}	-0.784^{***}	0.435^{***}	-0.141^{**}
Air-filled porosity (*Eg*)	0.767^{***}	0.702^{***}	-0.352^{**}	0.230^{***}
Oxygen diffusion rate (*ODR*)		0.587^{***}	-0.289^{***}	0.304^{***}
Redox potential (*Eh*)			-0.539^{***}	0.290^{***}
Fe^{+2} content				-0.145^{**}

**– P<0.01; ***– P<0.001; CAT – catalase activity.

Oxygen diffusion rate increased with air-filled porosity but decreased with increasing soil water content (Fig. 3a-b). Soil water content exceeding 40% (v/v) resulted in lowering of O_2 diffusion below approx. 30 μg m^{-2} s^{-1} (Fig. 3b). This *ODR* value of about 30 μg m^{-2} s^{-1} has previously been shown also to be a critical threshold for root growth [9]. Redox potential (*Eh*) was negatively related to soil water content but positively to *ODR* at its values <40 μg m^{-2} s^{-1}, and remained above 300 mV when *ODR* exceeded this value (Fig. 3c-d). Concentration of reduced iron was low (<29 mg kg^{-1}) in drier soil (*ODR*>30 μg m^{-2} s^{-1}), but increased up to 360 mg kg^{-1} below 30 μg m^{-2} s^{-1} (Fig. 3e-f). Similar results were observed for other soils [9,24].

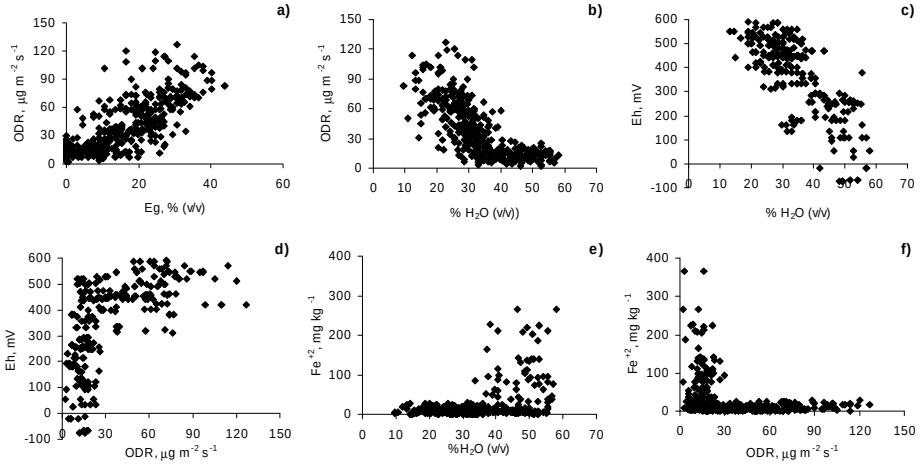

Fig. 3. Relations between aeration parameters in the Orthic Luvisol conditioned at different air-water status (results of three 14-day stresses)

Multiple regression analysis indicated *ODR* and *Eh* (but not the water, air (*Eg*) and Fe^{+2} – contents) to be significant for modification of catalase activity (F-ratio for full regression = 15.1, P<0.001, CAT-catalase activity):

$$CAT = 5.99 + 0.008\ ODR + 0.001\ Eh \qquad (1)$$

This simple model, based on experimental results, suggests that catalase activity is relatively stable in soil. The effects of O_2 diffusion rate and redox potential, although statistically significant, play a small part in the determination of the level of the enzyme activity. However, considering the periodical changes between flooding and drainage in field soil, the capability of soil microbes to retain this 'aerobic' activity under anaerobiosis seems to be important for their adaptation. Moreover, the O_2-dependent activity occurs in the oxic-anoxic interfaces that can be expected in soil aggregates and biofilms, as well as in unstable aerobic soil layer overlying bulk soil under flooding.

Soil catalase activity versus soil aeration properties are illustrated in Figure 4 (results presented as averages for particular experimental treatments). The catalase activity was inhibited by soil hypoxia, as was reflected by lowering of the activity with increases of both soil water and Fe^{+2} contents (Fig. 4a-b). In turn, the activity was stimulated by improvement in soil aeration, and increased with increasing air-filled porosity, oxygen diffusion rate, and redox potential (Fig. 4c-e).

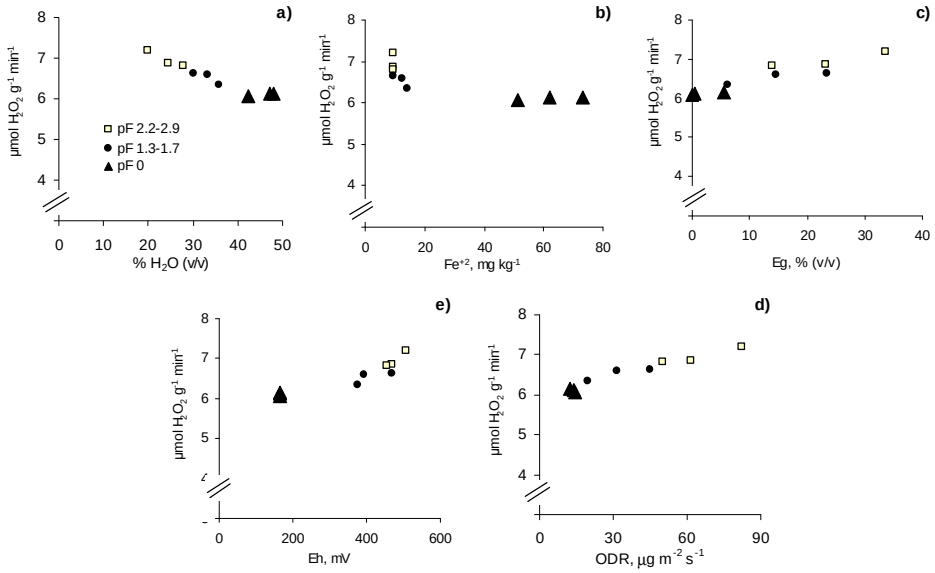

Fig. 4. Soil catalase activity versus parameters under investigation – averages for experimental treatments at soil pF 2.2-2,9 (□); pF 1,3-1,7 (●); and pF 0 (▲)

Aerobic bacteria use catalase for protection against by-products formed during oxygen-dependent metabolism. Thus, catalase takes part in pathways which are directly related to the aeration status of the microbial growing medium. We observed that over 14-day flooding of the Orthic Luvisol, deactivation of catalases was not complete and/or there were still active microbes equipped with this defensive mechanism. Catalase has been shown to be very stabile in soil [1]. Introduced to the soil, it is immobilized on the surface of clay minerals or associated with organic colloids [21,22,27]. Thus, the ability to decompose exogenous H_2O_2 under soil hypoxia might also involve the catalytic action of 'abiotic' catalases. Extracellular enzyme activity is not related to microbial activity and, therefore, not subjected to repression or induction and, probably, not sensitive to environmental conditions affecting the physiological state of the micro-organisms [20].

Most "strictly" anaerobic bacteria lack superoxide dismutase (that contributes to generation of indigenous H_2O_2) and catalase activities (that destroys H_2O_2). However, some anaerobes evolved systems that protect cells against hydrogen peroxide which, by being freely diffusible through cell membranes, is a strong oxidative stress-generating agent. In the heterogeneous soil system, various micro-sites occur, from aerobic to micro-aerobic, and anaerobic. Antagonistic processes (e.g., oxidation and reduction) take place simultaneously. The distri-

bution and composition of these microenvironments changes dynamically due to the impact of abiotic factors, and also as a result of the vital activity of soil organisms (e.g., meso- and macro-fauna, plant roots). For facultative anaerobes, an important mechanism of metabolism regulation is the induction of catalase during the anaerobic to aerobic transition [11,12].

In our experiment, the soil, packed in open pots, was sampled at the surface (0-5 cm) with possible gas exchange to the atmosphere. The average *Eh* values in flooded variants were relatively high, about +160 mV. However, greater anaerobiosis was developed locally, as negative *Eh* values down to –75 mV, were measured. The 'ability' of hypoxic soil to destroy exogenous H_2O_2 probably resulted from the sum of the activities of catalases originating from facultative and aerotolerant anaerobes, microaerophilic micro-organisms, as well as those enzymes that were still active outside living cells. Thus, catalase activity measured in soil gives indications of the *potential* capacity of soil to carry out this specific reaction [5]. Catalase is one of the most efficient enzymes known, meaning that H_2O_2 generated during respiratory processes would be rapidly converted into oxygen and water. The significant defensive role for the catalase enzymes also could be the reason for the relatively narrow range of catalase activity (14-fold) found by Levi-Minzi *et al.* [16] for 14 different soils, as compared to the wide ranges observed for hydrolytic enzymes (i.e., 577-fold for β-glucosidase).

In conclusion, the combination of compaction level and soil water potential in an Orthic Luvisol soil in a pot experiment resulted in changes of soil aeration status, which was reflected by wide ranges of air filled porosity, oxygen diffusion rate, redox potential, as well as the content of reduced Fe. Soil compaction (in the range of 1.2-1.5 Mg m^{-3}) significantly reduced *Eg*, *ODR* and *Eh*, but did not significantly change [Fe^{+2}] and catalase activity. Soil water potential (in the range of pF 0 to 2.9) significantly affected all the properties, including catalase activity. Soil catalase activity increased under well-aerated conditions and was linearly positively correlated with *Eg*, *ODR* and *Eh*, while negatively correlated with volumetric water content (linearly) and Fe^{+2} content (curvilinearly). Oxygen diffusion rate showed typical positive linear relationship with *Eg* and negative with volumetric water content with a threshold value at 40% v/v. Redox potential dropped at *ODR* <30 μg m^{-2} s^{-1}, reduced Fe content increased with *Eh* < 300 mV. Oxygen diffusion rate and redox potential provided the best relationship between catalase activity and soil aeration status.

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WPŁYW STANU NATLENIENIA NA AKTYWNOŚĆ KATALAZY W GLEBIE (ORTHIC LUVISOL)

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S t r e s z c z e n i e. Badano wpływ stanu natlenienia gleby (Orthic Luvisol) na aktywność katalazy w doświadczeniu modelowym z udziałem pszenżyta (Triticale cv. "Jago"). Wilgotność gleby o trzech stopniach zagęszczenia (1,2; 1,35 oraz 1,5 $Mg \cdot m^{-3}$) utrzymywano w zakresie wody łatwo dostępnej dla roślin (pF 2,2-2,9). W trzech fazach wzrostu roślin zastosowano stresy tlenowe – okresy niedotlenienia gleby poprzez podniesienie wilgotności gleby do pF 1,3-1,7 i pF 0 (zalanie wazonów). Parametry stanu natlenienia gleby (porowatość powietrzna – Eg; wydatek dyfuzji tlenu – ODR, potencjał redoks – Eh; zawartość żelaza zredukowanego [Fe^{+2}]), modyfikowane przez wilgotność i zagęszczenie gleby, wykazywały istotne powiązanie. Aktywność katalazy, enzymu związanego z metabolizmem tlenowym drobnoustrojów glebowych, była obniżona w glebie niedotlenionej o około 16% w stosunku do materiału kontrolnego. Zależność aktywności katalazy od stanu natlenienia gleby najlepiej opisywały wskaźniki ODR i Eh.

S ł o w a k l u c z o w e: stan natlenienia gleby, aktywność katalazy, niedotlenienie gleby