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Original Research

Dehydrogenase Activity Response to Soil Reoxidation Process Described as Varied Conditions of Water Potential, Air Porosity and Oxygen Availability

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Abstract

This paper analyzes the effects of soil reoxidation, expressed in terms of water potential (pF), air porosity (Eg) and oxygen availability (ODR), on soil dehydrogenase activity (DHA). Investigated soil samples were collected from the surface layer (0-20 cm) and subsoil (50-60 cm) of *Rendzina Leptosols*, *Eutric Histosol* and *Eutric Fluvisol* soils. All the examined factors varied widely in the tested material – DHA decreased whereas ODR and Eg increased with higher soil water tension. A close relationship, described by significant negative correlations between oxygenation indicators (pF, ODR, Eg) and DHA, was stated. To sum up the foregoing observations, we confirmed that dehydrogenases are sensitive enzymes, indirectly dependent on soil aeration status.

Keywords: dehydrogenase activity, oxygen availability, water retention, soil reoxidation

Introduction

Life in the soil environment, as well as land use, is related to alternate cycles of humidification and drainage. Soil reoxidation phenomenon is connected with reversion to aerated conditions following its flooding. During this process aeration factors such as Eg, Eh, and ODR change and these fluctuations have an effect on the metabolism of microorganisms and their enzymatic activities [1-3]. Recently, in Poland there was a progressive tendency for flooding or long-lasting periods of drainage. Due to this fact, it is important to study processes that occur during this time in the soil environment.

Soil water is not only essential for life processes of plants and microorganisms, but it also has many interacting components that, individually or in combination, affect biological systems and their activities [4-6]. These effects may arise from the potential energy of the water *per se* or from the indirect effects of water potential or water content on such factors as gas or solute diffusion and soil strength [7]. Thus, water retention is a basic hydrophysical characteristic of soil that can be described by the dependence between soil water content and soil water potential [8, 9]. Soil water content as a function of the soil water tension is described by pF curve [10], which provides information about the water retention ability by the soil pores at any given water tension, or conversely, how tightly water is held between soil aggregates. For more than 50 years the traditional method of pressure chambers has been mostly used to obtain the soil retention curve [10-12].

The space of soil pores is reversibly filled by water or air, depending on soil water potential, which influences soil

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Table 1. Basic characteristics of the investigated soil materials.

Soil type	Location	Depth [cm]	Granulometric composition [%]			C org [%]	pH [H_2O]
			1-0.02 [mm]	0.02-0.002 [mm]	<0.002 [mm]		
Rendzina Leptosols	Bezek SE Poland	0-20	59	17	24	0.89	7.95
		50-60	67	17	16	0.17	8.06
Eutric Histosol	Grzybowo NW Poland	0-20	76	12	9	8.34	6.07
		50-60	79	18	6	0.60	6.99
Eutric Fluvisol	Wolica SE Poland	0-20	60	14	26	8.59	7.04
		50-60	32	43	25	8.19	7.41

aeration status. This parameter is the most important determinant of soil productivity governed by two processes, namely:

(a) transport of oxygen from the atmosphere into the soil (atmospheric air contains, by volume, 20.5% O_2 whilst soil air is 0-20%), and
(b) biological consumption of oxygen either by microbial organisms and plant roots, or by respiration and chemical reactions [13].

A minimum air-filled pore space of 10% by volume is commonly considered necessary for adequate aeration [9, 10]. It also has been shown experimentally that ODR satisfactorily reflects the supply of oxygen to the plant roots [4, 7, 14].

The activity of soil enzymes is commonly believed to be sensitive to pollution and has been proposed as an index of soil degradation [15-17]. Among all enzymes existing in the soil environment, DHA are used as an indicator of overall microbial activity, because they occur intracellularly in all living microbial cells and are linked with microbial oxydoreduction processes [18-21]. Dehydrogenase (EC 1.1.1.1.) plays a significant role in the biological oxidation of soil organic matter by transferring protons and electrons from organic substrates to inorganic acceptors [18, 20-23]. For this reason we impose the hypothesis that DHA might be used not only as an index of soil pollution, but most of all as an indicator of oxygen deficiency (hypoxic and anoxic soil conditions) during the return of soils to a well aerated state (reoxidation process).

The aim of this study was to find the response of soil DHA to variable conditions of pF, Eg and ODR of selected soils, as a consequence of the reoxidation process.

Experimental Procedures

Description of Soils

The study was performed on three types of soils (FAO): *Rendzina Leptosols, Eutric Histosol,* and *Eutric Fluvisol* (Table 1) taken from two different depths (0-20 cm, and 50-60 cm) provided by the Bank of Polish Soil Samples [24].

The laboratory experiments were performed according to the diagram presented in Fig. 1.

Richards' Method for Determination of Soil-Retention Curves

A stainless-steel pressure chamber containing a porous plate saturated with water at the bottom at atmospheric pressure was used [25]. Soil samples were transferred on the plate inside the chamber in order to obtain the hydraulic contact between a sample and the porous plate. The chamber was closed and the appropriate air pressure *P* is applied to it, driving away the soil water retained at pressures below *P*, until equilibrium is reached [25]. Therefore, at each equilibrium state, the pressure applied to the soil sample represents the value of the matric potential for the respective water content.

At the beginning of the experiment soil samples in plastic cylinders (height 4.7 cm, diameter 3.2 cm) were preincubated under flooded conditions (10 days). Subsequently, soil samples were placed on water-tension plates, taken from the laboratory set LAB °12 (Soil Moisture Equipment Company, USA) and the pressure was applied for the following water potentials (pF): 0, 1.5, 2.2, 2.7, and 3.2, corresponding with the range of available water, and usefulness for microorganisms and plant roots. The time needed for soil samples to reach the pF values varied from 19 (pF 0) to 26 (pF 3.2) for *Rendzina Leptosols*, from 23 to 30 days for *Eutric Histosol* and from 17 to 24 days for *Eutric Fluvisol*.

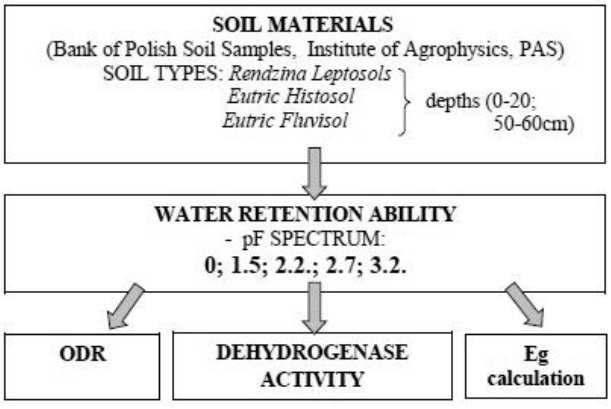

Fig. 1. Scheme of the laboratory experiment.

ODR Measurement and Eg Calculation

After determination of pF values, ODR was measured using an ODR-meter manufactured by the Institute of Agrophysics, Polish Academy of Soil Sciences (Lublin), using the Lemon and Ericcson method [26]. The ODR technique consists of the measurement of the electric current intensity corresponding to the reduction of oxygen on a platinum cathode placed in the soil and negatively polarized with respect to the reference electrode (calomel). As oxygen is consumed at the microelectrode, more oxygen needs to diffuse radially to the electrode in response to the accumulated gradient. This is analogous to oxygen consumption by respiration of root surface or by microbial respiration [26]. Four platinum wire electrodes (0.5×4 mm) were placed at a depth of 2 cm and polarized to -0.65 V versus saturated calomel electrode for 4 min. The data were recorded in three replicates for each sample.

Eg factor was calculated taking into account water content, soil density, and solid phase density, according to the method described by Stępniewski et al. [27].

DHA Measurement

Soil DHA was tested using 2,3,5-triphenyltetrazolium chloride (TTC), according to the method adopted from Casida et al. [28]. The soil samples (6 g of soil + 2 mL of distilled water + 120 mg $CaCO_3$) were left to react with 1 mL of 3% TTC solution at 30ºC for 20h and then they were extracted with ethanol and incubated for 1h in the dark. Absorbance (λ=485 nm) was measured using UV-VIS U-2001 (Hitachi) instrument. DHA was expressed as μg TPF g^{-1} min^{-1}. All measurements were triplicated and calculated on the basis of the oven-dry (105ºC) soil mass.

Data Analysis

Statistical analysis was made with Statistica 8.0 software (STATSOFT, USA). One-way ANOVA test was used to investigate significant (P<0.05) effects of aeration factors (pF, ODR, Eg) on soil DHA.

Results and Discussion

Soil Ability to Retain Water

The relationships between soil water content (%, v/v.) and water potential (pF) for *Rendzina Leptosols, Eutric Histosol,* and *Eutric Fluvisol* are presented in Figs. 1A, 1B and 1C, respectively.

The amount of water bound with different forces in a unit of soil volume is especially useful, as it defines the possibility of water uptake by plants from the soil volume covered by the root system, and permits the definition of water resource balance in different soil horizons [9]. Water content in the surface layer (0-20 cm) of *Rendzina Leptosols* (Fig. 1A) ranged from 41% at pF 0 to 13% at pF 3.2, whereas in subsoil (50-60 cm) it reached 24% (pF 0) and 9% (pF 3.2). Similarly, water retention in the surface layer of *Eutric Histosol* (Fig. 1B) was estimated at 40% (pF 0) and decreased during reoxidation to 9% (pF 3.2). Meanwhile, in the deeper layer of the soil profile water content varied between 23% and 3% for pF 0 and pF 3.2, respectively. An equally high capability of *Eutric Histosol* for water maintaining (46-5%) was noted by Włodarczyk and Witkowska-Walczak [7], as well as Walczak et al. [12]. Among of investigated soils, *Eutric Fluvisol* had the smallest ability for water retention (Fig. 1C). Water content in the surface layer was registered as 27% (pF 0) and 13% (pF 3.2), whilst in the layer of 50-60 cm it achieved values from 32% to 14% for pF 0 and pF 3.2.

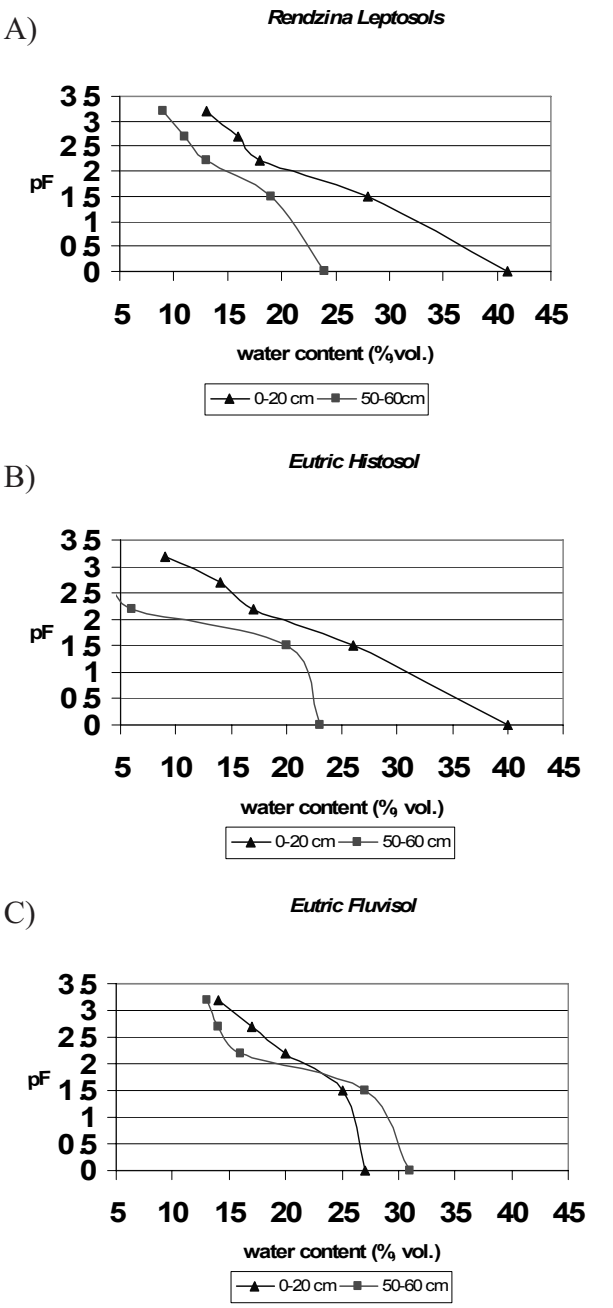

Fig. 1. The relationship between soil water content (%, v/v) and water potential (pF) in the *Rendzina Leptosols* (A), *Eutric Histosol* (B), and *Eutric Fluvisol* (C).

Soil Aeration Factors Influencing DHA

Based on performed measurements, it was found that pF constitutes a significant factor, determining ODR in the soil environment, as well as its DHA level ($P<0.01$). The reoxidation process, occurring in the direction from pF 0 to pF 3.2, was the reason for the inhibition of DHA and stimulation of ODR level.

Response of DHA to varied values of soil aeration, expressed by pF and ODR for *Rendzina Leptosols, Eutric Histosol,* and *Eutric Fluvisol* are presented in Figs. 2A, 2B and 2C, respectively.

Oxygen availability in relation to the soil water potential and DHA indicates that ODR values at the surface layer (Fig. 2A) fluctuated from 8.45 to 84.3 μg O_2 m^{-2} s^{-1} at pF 0 and 3.2, respectively. At a deeper layer of *Rendzina Leptosols* profile (50-60 cm), ODR reached much higher levels from 13 till to 110.92 (μg O_2 m^{-2} s^{-1}), as follows for pF 0 and 3.2. Stępniewska and Wolińska [8] found a similar tendency for higher oxygen availability in the deeper layers, rather than in surface of the *Eutric Cambisol* soils, whereas Walczak et al. [12] observed an analogous trend in the *Mollic Gleysol*. Several explanations have been offered for this enigma. It may be caused by methodical limitations,

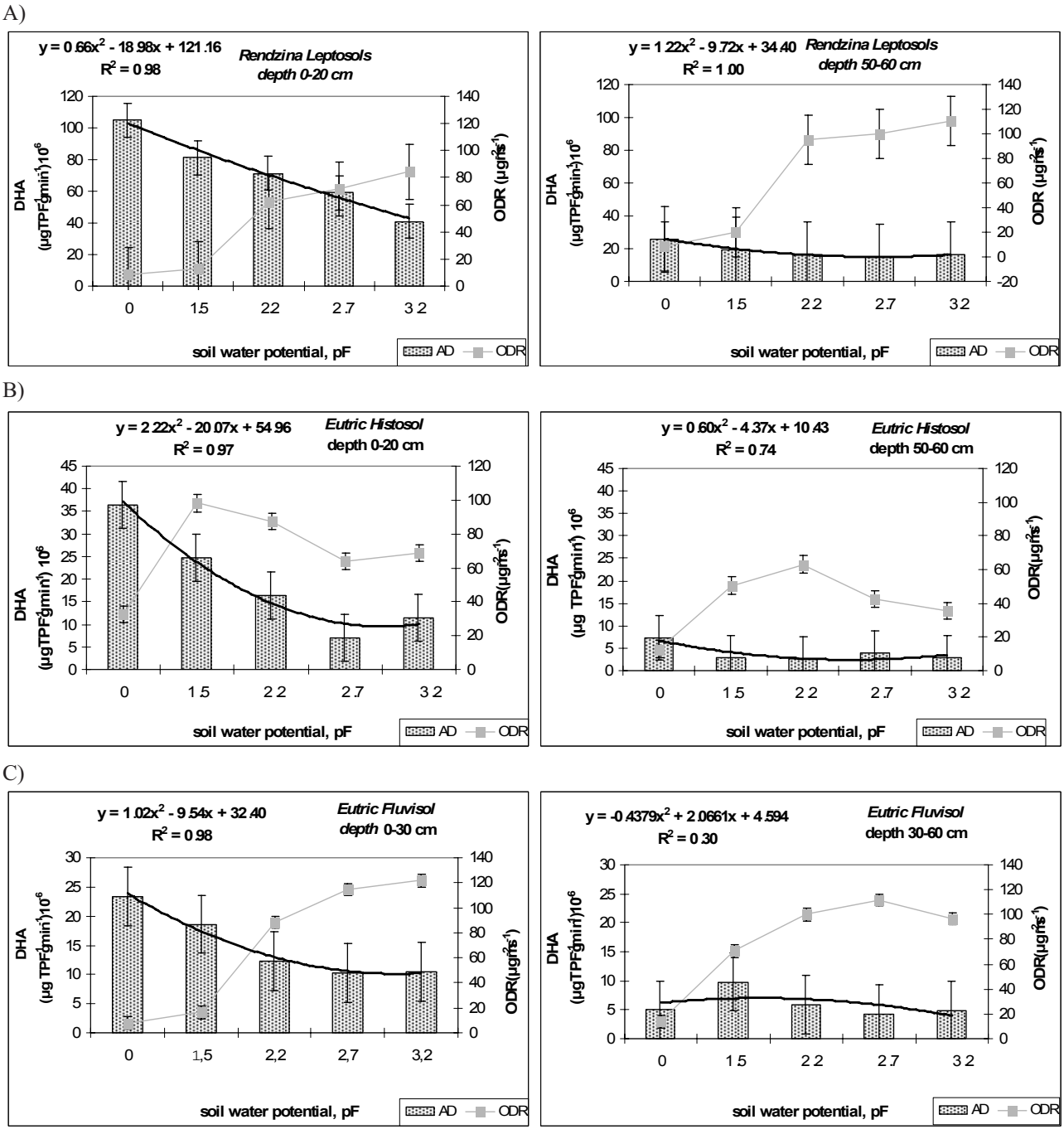

Fig. 2. The response of soil DHA to varied aeration factors (pF and ODR), at different depths of *Rendzina Leptosols* (A), *Eutric Histosol* (B) and *Eutric Fluvisol* (C) during the reoxidation process. Averaged values of three replicates with standard deviations are presented.

as the water barriers or water films present on the surface of the electrode could be broken off. Quite likely, the explanation involves the differences in granulometric composition of analyzed soil samples (Table 1), as the fact that large granulation favorable for forming of aeration pores was noted in the subsoil layers.

Soil DHA calculated in *Rendzina Leptosols* reached its maximum of $105 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1} at total water capacity (pF 0, Fig. 2A). A significant linear decrease of DHA, accompanied by water potential increase, was observed ($P<0.05$). Soil DHA at pF 3.2 was lower by 60.86% in comparison to the activity estimated at pF 0. In the case of *Rendzina Leptosols* subsoil (50-60 cm), much lower values of DHA were registered (Fig. 2A). At pF 0, DHA equaled $26.6 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1}, and this value was decreased by 74.6% in relation to the same soil humidity at surface layer (0-20 cm). At different levels of pF, DHA varied as follows: 16.4, 15.1, and $16.3 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1} for pF 2.2, 2.7, and 3.2, respectively (Fig. 2A).

DHA of the *Eutric Histosol* at varied soil water potential, as well as oxygen availability, is presented in Fig. 2B. Soil DHA in surface layer samples reached the level of $36.3 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1} at pF 0, and dropped to the value of $11.4 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1} at pF 3.2. In comparison with highly enzymatic active *Rendzina Leptosols, Eutric Histosol* soil seemed to be 65% and 89% less active in DHA, for pF 0 and 3.2, respectively. Subsoil of *Eutric Histosol,* characterized by low DHA, varied from 7.25 to $2.86 \cdot 10^{-6}$ µg TPF $g^{-1}min^{-1}$ for pF 0 and pF 3.2.

Among tested soils, *Eutric Fluvisol* displayed the lowest values of soil DHA (Fig. 2C). Full water-saturated soil (pF 0) resulted in DHA at surface layer at the level of $23.4 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1}, then a drop in enzyme activity until $10.5 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1} at pF 3.2 was registered. Much lower values of DHA, with its maximum at pF 1.5, equaled $9.78 \cdot 10^{-6}$ µg TPF g^{-1} min^{-1}, at the layer of 50-60 cm were noted (Fig. 2C). The highest level of ODR at the surface layer of *Eutric Fluvisol,* at water potential pF 3.2-121.97 µg O_2 m^{-2} s^{-1}, was stated, whereas the lowest values of 2.88 µgO_2 m^{-2} s^{-1} of ODR at pF 0 were found. A similar tendency at the deeper layer of *Eutric Fluvisol* was observed, where ODR values varied between 4.16 and 96.47 µg O_2 m^{-2} s^{-1} for pF 0 and pF 3.2, respectively. Much lower values of DHA in *Eutric Fluvisol*, in comparison to other investigated soils, might be caused by the small ability of this kind of soil for water retention capacity (Fig. 1C). The wide range of water content (3-41% v/v) was a strong physical determinant of DHA. Brzezińska et al. [18] found that DHA increased with water supply, which is comparable with results presented in the current study. An increase of DHA at flooded soils was signaled as well by Stępniewski et al. [4], Brzezińska et al. [18], Lee et al. [29], and by Hinojosa et al. [30]. The decline of DHA with an increase of pF value from 0 to 3.2 could be explained by the fact that flooding of soil with water significantly increased the electron transport system (ETS). Dehydrogenases, however, are responsible for electron transport and carry out a broad range of activities that are reliable for oxidation, i.e. dehydrogenation of organic matter [31]. Under different soil moisture contents aerobic and anaerobic, microbial activity must be expected. The main source of soil dehydrogenase is anaerobe, which propagates rapidly under conditions of higher soil moisture content [4, 18, 32], which significantly alters the microbial population activity [33]. Thus, the high DHA with increasing soil moisture may be caused by increased enzymes released into the soil because of faster turnover of the microbial biomass when more water is available [32]. In the case of low soil moisture content (i.e. pF 3.2), the decrease of DHA may be due to extreme dryness, which becomes unfavorable for most microbial communities; few could survive in the soil [33].

Table 2. Statistical significance of differences between DHA and tested parameters described by correlation coefficient (R) (95% LSD method, n=15).

DHA response	depth [cm]	pF	ODR	Eg
Rendzina Leptosols	0-20	-0.98***	-0.90**	-0.96**
	50-60	-0.95**	-0.84*	-0.70**
Eutric Histosol	0-20	-0.95***	-0.41*	-0.34*
	50-60	0.65 n.s.	-0.43*	-0.39*
Eutric Fluvisol	0-20	-0.97***	-0.96**	-0.97**
	50-60	-0.22 n.s.	-0.16 n.s.	-0.43*

*, **, *** - indicate significance at the 5, 1 and 0.1% level, respectively,
n.s. – not significant differences.

Correlations between DHA and pF, ODR, Eg

DHA was negatively correlated with tested aeration parameters (pF, ODR, Eg). Air porosity (Eg) for *Rendzina Leptosols, Eutric Histosol,* and *Eutric Fluvisol* ranged as follows: 0.072-0.43; 0.11-0.23; 0.071-0.29 m^3 m^{-3}. During the reoxidation process from pF 0 to pF 3.2, growth of Eg was noted. Statistical relationships between DHA and measured aeration factors are presented in Table 2.

The significant influence ($P<0.05$) of tested soil aeration factors on DHA was stronger in the surface layers than in subsoils. Higher values of DHA were noted with lower Eg and ODR levels, therefore negative correlations were stated. Insignificant differences were found only in the subsoils of *Eutric Histosol* and *Eutric Fluvisol* in the case of pF and ODR, respectively. Low oxygen availability (2.8-25 µg O_2 m^{-2} s^{-1}) ranged below its critical values (35 µg O_2 m^{-2} s^{-1}), was favorable and optimal for DHA. Our results are in agreement with the work of Stępniewski et al. [4], Brzezińska et al. [18], and Yang et al. [34].

DHA of the investigated soil samples originating from the surface layers, was significantly higher than those noted in the subsoils ($P<0.001$). This enzymatic activity was reduced even by 83% at a depth of 50-60 cm, in comparison to the surface part of the profiles. Brzezińska [35] stat-

ed 25-fold of DHA in the soil material taken from surface layers rather than in the subsoils. Similar observations were published by Stępniewski et al. [4], Yang et al. [31] and Skawryło-Bednarz [36].

Conclusions

It has been demonstrated that soil water potential (pF), oxygen availability (ODR), and air porosity (Eg) influence soil dehydrogenase activity (DHA). This can be explained by their indirect effect on the soil oxidation status.

Water potential (pF) values ranged from 41% (pF 0) to 13% (pF 3.2), 40-9%, and 46-5%, in the surface layers of *Rendzina Leptosols, Eutric Fluvisol* and *Eutric Histosol,* respectively. The trend of capability of retaining water, among investigated soils, was arranged as follows: *Orthic Rendzina* > *Eutric Histosol* > *Eutric Fluvisol*. Increase of pF value, in the view of progressing reoxidation process, was strongly correlated with a decrease in DHA (negative relationship, $P<0.01$).

ODR at soil surface layers (0-20 cm) fluctuated from 8.45 to 84.3 ($\mu g\ O_2\ m^{-2}\ s^{-1}$) at pF 0 and pF 3.2, respectively, and exhibited a negative correlation ($P<0.05$) with DHA.

Air porosity (Eg) varied widely for the studied soils in the range from 0.071 $m^3\ m^{-3}$ (pF 0) to 0.43 $m^3\ m^{-3}$ (pF 3.2), and was also negatively correlated ($P<0.05$) with DHA at each of investigated soil types and depths.

The consequence of the inverse relationship of DHA with the aeration parameters could be the inhibition of enzymatic activity with an increase of water potential within the intervals from 105 to $10.5 \cdot 10^{-6}$ ($\mu g\ TPF\ g^{-1}\ min^{-1}$) at pF 0 and 3.2, respectively. The negative relationships ($P<0.05$) were found between DHA and each of investigating soil aeration factors (pF, ODR, Eg). Insignificant correlations (DHA-pF; DHA-ODR) were stated only in *Eutric Histosol* and *Eutric Fluvisol* subsoil.

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