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Effect of soil compaction on dehydrogenase activity in bulk soil and rhizosphere**

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A b s t r a c t. The effect of soil compaction on dehydrogenase activity of the bulk soil and soil rhizosphere surrounding roots of spring wheat were investigated. The measurements were made at different depths of layered soil profile. The highest dehydrogenase activity was measured in heavily compacted soil, probably as an effect of increased amount of exudates which helps root to growth in compacted soil. The highest difference between dehydrogenase activity in bulk soil and the rhizosphere occurred in the most compacted soil. General decrease of dehydrogenase activity with depth was observed in all objects.

K e y w o r d s: dehydrogenase activity, soil compaction, rhizosphere, spring wheat

INTRODUCTION

Soil management practice by influencing microbial communities in soil change soil enzyme activity (Fraser *et al.*, 1988; Jezierska-Tys and Frąc, 2009) and dehydrogenase activity (DHA) is often used to study the influence of anthropogenic activity on soil health (Singh and Kumar, 2008). Changes of dehydrogenase activity reflect changes in soil microbial activities (Schäffer, 1993; Włodarczyk, 2000), however the relation between soil compaction and microbial activity is complex and depend on soil history (Whalley *et al.*, 1995).

Strength increase of the soil caused by soil compaction affects plant growth in many ways. According to plant species and soil type, the compaction decreases root elongation for soil penetration resistance values above 0.8-5.0 MPa (Pabin *et al.*, 1998). The slowed root growth in heavy soils is directly caused by external pressure induced by the compacted soil on root apex. On the other hand, soil compaction determines contact area between roots and soil environment and it helps plant to absorb water and nutrients. Soil compaction affects soil hydraulic properties. The low soil hydraulic conductivity may induce water shortage to plant growth especially for high transpiring plants. The restrictions to plant growth in compacted soil are also caused by oxygen deficit. Soil oxygenation status depends on air-water conditions and influences plant growth (Lipiec and Stępniewski, 1995).

The rhizosphere, cylindrical volume of soil surrounding roots, is recognised as one of the most important compartments of terrestrial ecosystems, due to its major influence on biogeochemical cycles (Raynaud, 2010). The rhizosphere is a dominant site of microbial metabolism in soil and increases the levels of enzymes, creating favourable conditions for root growth and function (Skwaryło-Bednarz and Krzepiłko, 2009). Plant exudates may regulate the soil microbial community in their vicinity, change the chemical and physical properties of the soil (Iijima *et al.*, 2000; Walker *et al.*, 2003).

The mucilage exudation and sloughing of root cap cells may be a way in which plants decrease friction between root tip and a soil (Bengough *et al.*, 1997). These exudates may enhance growth of the microorganisms in the rhizosphere. Increasing nematode activity in rhizosphere with the increasing soil bulk density was explained by Griffiths *et al.* (1991) by intensive mucilage secretion in the compacted soil. Norton and Firestone (1991) found out that there are more microorganisms within 5 mm from roots than in bulk soil. Microbial populations on the rhizoplane, when plants were grown in compacted soil, were composed of high ratios of bacteria utilizing root exudates efficiently (Ikeda *et al.*, 1997). Increased content of organic carbon within the rhizosphere was linked to observed increase of dehydrogenase activity (Chu *et al.*, 2007; Lagomarsino *et al.*, 2009). The negative correlation between dehydrogenase activity and soil aeration was observed by Brzezińska *et al.* (2001b).

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Complex interactions between aeration, water status and soil biodiversity makes the effect of soil compaction on microbial activity difficult do study (Whalley *et al.*, 1995) and the impact of these factors on enzyme activity is not clear (Li *et al.*, 2002). The rhizospheres of neighbouring roots often overlap so it may be difficult to distinguish between them in dense root system. The fraction of rhizosphere decreases with decreasing root length density depending on the rooting depth and root system age.

The aim of the present study was to determine dehydrogenase activity in soil profile compacted to a different degree and to evaluate the differences in dehydrogenase activity between bulk soil and rhizosphere of wheat growing in variously compacted soil.

MATERIALS AND METHODS

The soil used in the experiment was Orthic Luvisol developed from silt formation (Table 1). Soil was taken from the field in the early spring from 0-20 and 20-40 cm depths. Then was sieved without drying through 4mm sieve, and manually compacted into 10 cm high cylindrical PCV tubes of a 15 cm diameter. Cylinders with soil were connected to create 40 cm high artificial soil profiles with soil density distribution corresponding to moderately and heavily compacted soil. The control soil profile was filled with loose soil. Soil taken from 0-20 cm depth was used for 0-10 and 10-20 cm layers of artificial soil profile, soil from 20-40 cm depth was used for layers 20-30 and 30-40 cm. The density in loose (L), control column was 1.31 Mg m^{-3}, in moderately compacted soil (MC) column soil density was 1.31 at 0-20 cm depth and 1.48 Mg m^{-3} at 20-40 cm depth, in heavily compacted soil (HC) to densities: 1.50 at 0-20 cm and 1.72 Mg m^{-3} at 20-40 cm depths.The soil penetration resistance was measured at soil moisture corresponding to -35 kPa of soil water potential using probe of 30° cone and 1.8 mm diameter. Results are an average penetration resistance measured at the distance of 9cm starting from 0.6 cm depth of each soil layer. The speed of probe and data collection rate were 1 mm s^{-1} and 100 readings s^{-1}, respectively.

Two spring wheat (var. Jasna) plants were grown in each soil column. The conditions during the 30th day long experiment were: 16/8 h day/night period, 22/16°C day/night temperatures, 75% air humidity, 5.3 klx light intensity, soil water potential: - 35 kPa.

Gas for CO_2 analyses was sampled at 0.05; 0.15; 0.25 and 0.35 m depths. Samples of soil air were analysed using gas chromatograph Shimazu GC14A. Oxygen diffusion rate (ODR) was measured at the same depths as CO_2 concentration using Pt electrodes. Both ODR and CO_2 concentration were measured at the last day of experiment before plant excision.

The soil was sampled (10 g) from each 10 cm soil layer from soil volume without any roots on 30th plant growth day. Rhizosphere soil was obtained in two steps: the roots were separated from the bulk soil by shaking gently (Fox and Comerford, 1992), soil still adhering to the roots was defined as rhizosphere soil and was removed using a dissecting probe (Benitez *et al.*, 2000). Dehydrogenase activity was determined by the TTC (2, 3, 5-triphenyl tetrazolinum chloride) method according to the modified method of Casida *et al.* (1964) and expressed as nmol TPF g^{-1} min^{-1}.

The root length was determined in each of soil layer, after washing them out of the soil. Roots were immersed in 3-4 mm layer of water in glass cuvette and scanned using flatbed scanner (Epson 3200 Photo) at 600 dpi. The scanned images were analysed using Scion Image software with macro procedure (Kimura *et al.*, 1999).

RESULTS AND DISCUSSION

The oxygen diffusion rate values (Fig. 1) indicate that in general oxygen stress did not occur in any of the treatments. ODR one of the indicators of soil aeration (Stępniewska and Wolińska, 2006) do not drop below value of 70 μg m^{-2} s^{-1}, that is known to be a indicator of beginning of oxygen stress for plants (Zawadzki, 2009). The lowest values of ODR observed in MC at 0.05 and 0.15 m and in HC at 0.25-0.35 m were probably caused by the oxygen use by the relatively long roots within 0-0.20 cm layers in MC (Fig. 2) or by lower air diffusivity in compacted soil in 0.20-0.40 m in HC. However, the method used in the experiment allowed only to measure ODR in unknown distance from roots. Experiments conducted on different status of soil aeration resulting from soil compaction (Brzezińska *et al.*, 2001a,b) indicate that DHA do not change notably for ODR ranging from about 50 to 150 μg m^2s^{-1} – the range of ODR that occurred in this experiment.

Carbon dioxide concentration in soil profile (Fig. 3) was within the range of 0.28-0.54% v/v. The lowest CO_2 concentrations occurred in 0-10 cm layer as a result of gas exchange between atmosphere and soil air, the highest, measured in

T a b l e 1. Basic characteristics of the soil

Depth (m)	Granulemetric composition (%, dia in mm)			$N\text{-}NO_3$	$N\text{-}NH_4$	$C_{org.}$ (%)
	1-0.1	0.1-0.01	0.01-0.001	(mg kg^{-1})		
0-0.2	31.0	44.0	25.0	10.35	8.30	1.21
0.2-0.4	27.5	42.5	30.0	7.92	7.20	0.51

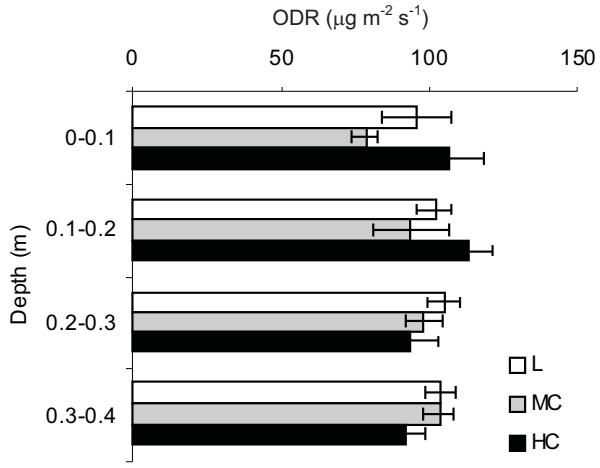

Fig. 1. Oxygen diffusion rate at the specified depths of soil columns. Horizontal bars represent ±SE. L – column with loose soil, MC – density corresponding to moderately compacted soil, HC – density corresponding to heavily compacted soil.

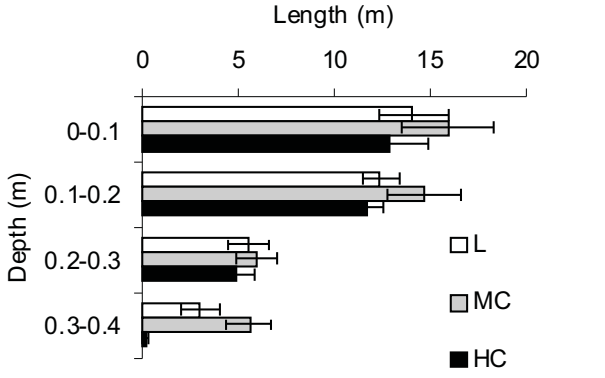

Fig. 2. Root length at specified depths. Abbreviations as on Fig. 1.

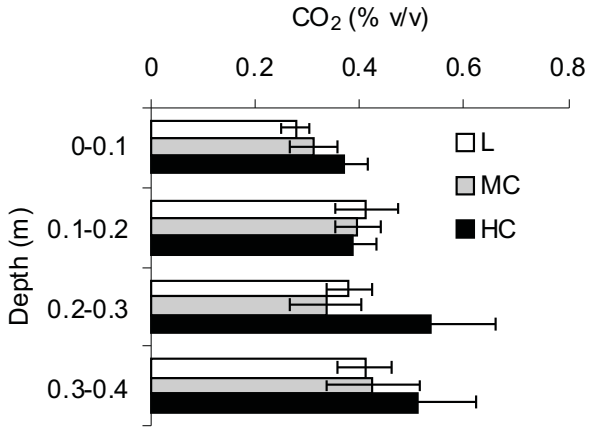

Fig. 3. Carbon oxide (2) concentration in soil air at the specified depths of soil columns. Abbreviations as on Fig. 1.

0.20-0.40 cm layers of HC soil columns, were a consequence of low rate of gas exchange with atmosphere caused by lower soil porosity (La Scala *et al*., 2009).

The root length distribution with depth at the 30th day of wheat growth is presented in Fig. 2. The differences between objects are the result of different soil compaction which reduces root growth rate by increased soil impedance to root growth. Impedance to root growth may be related to soil penetration resistance by steel cone, measurements of penetration resistance are presented in Table 2. Penetration resistance of soil layers with density equal to 1.3 and 1.5 Mg m^{-3} were below value of 3 MPa usually assumed as a value above which root growth is impeded (Hakansson and Lipiec, 2000). 20-40 cm layers of HC soil column had penetration resistance above 3MPa, restricting root growth, what was reflected in shorter roots within these layers.

The average values of DHA measured in bulk soil are generally in a good agreement with results of Włodarczyk (2000) (Fig. 4). Studies conducted on the same soil collected from 0-20 cm depth in March, similarly as in our experiment, showed DHA on the level of about 0.02-0.03 nmol TPF g^{-1} min^{-1}. Studies of Brzezińska *et al.* (2001b) on barley growing in the same soil with bulk density of 1.2 Mg m^{-3} at 15-80 kPa water potential resulted in soil DHA on the average level of 0.029 nmol TPF g^{-1} min^{-1}. DHA of a bulk soil was not dependent on soil density at specified depth in this experiment, also as in experiment on triticale growing in artificially compacted soil with density ranging from 1.20- 1.50 Mg m^{-3} (Brzezińska *et al.,* 2001a).

The result shows a decline of enzyme activity with soil depth similarly as in studies on natural soil profiles (Aon *et al.,* 2001; Niemi *et al.*, 2005). Dehydrogenase activity in bulk soil was decreasing with increasing depths in all objects from 0.32-0.35 in 0-0.1 m layer down to 0.10-0.15 in 0.3-0.4 m layer. The course of decrease of DHA in bulk soil with depth was similar in L, MC and HC objects. The observed drop of DHA below 0.2 m may be a result of lower content of organic carbon in these soli layers (Table 1). It is possible that measurement that aimed to measure DHA in bulk soil, were also within range of a rhizosphere, especially in the layers 0-10 and 10-20 cm with long roots (Fig. 2), as for dense root systems clear bulk soil is relatively rare (Raynaud, 2010).

The rate of DHA decrease with depth was generally steeper in rhizosphere than bulk soil what can be seen from fitted trend lines. Decrease of DHA with depth described by slope of fitted line were within -0.0079 and -0.0070 for bulk

T a b l e 2. Soil penetration resistance (PR) for different bulk density. Standard errors are given in the brackets

Bulk density (Mg m^{-3})	1.30	1.50	1.72
PR (MPa)	1.13 (0.18)	2.77 (0.32)	3.83 (0.52)

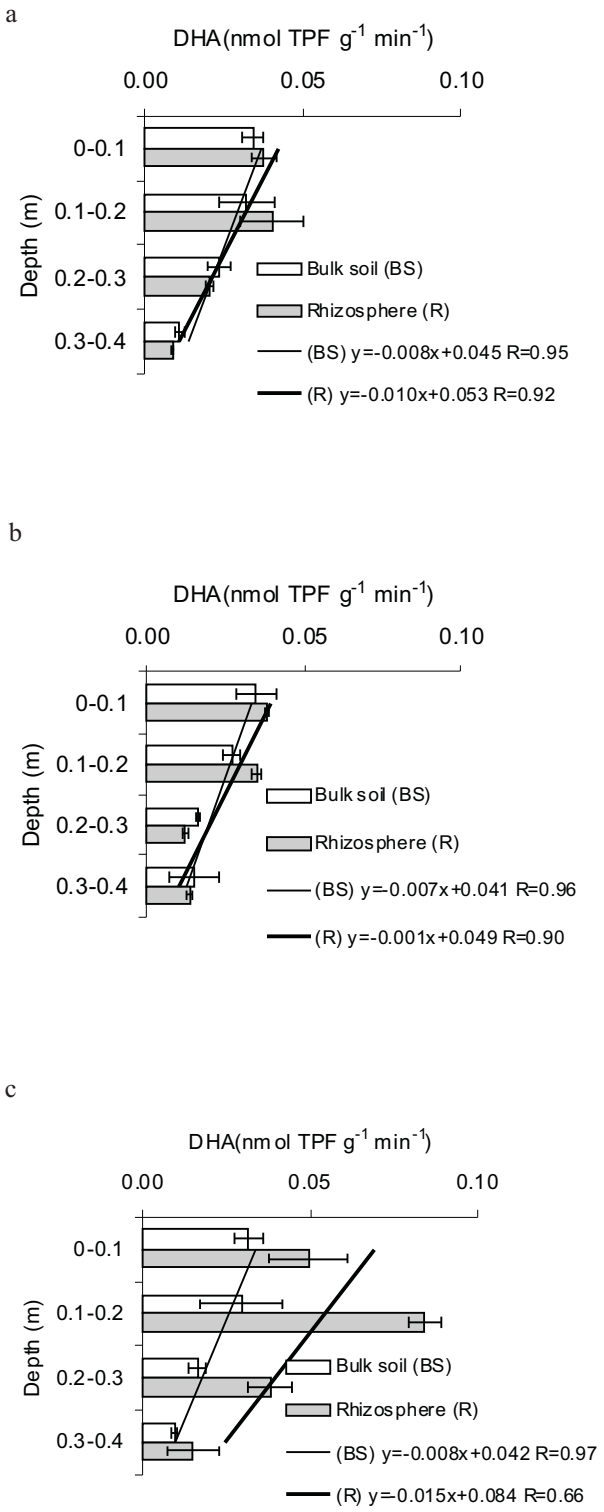

Fig. 4. Dehydrogenase activity mesured in the soil and rhizosphere. Abbreviations as on Fig. 1.

soil, larger differences in slope of a trend lines were for DHA in rhizosphere ranging from -0.0149 to -0.0096. The steepest decrease of DHA was observed in heavily compacted soil HC as in bulk and rhizosphere soil, being a consequence of the lowest DHA in 20-40 cm layers of bulk soil and highest DHA in the rhizosphere in 0-20 cm layers as compared to other treatments.

DHA in rhizosphere were higher than in bulk soil in any of the treatments in 0-20 cm layers and in all 0-40 cm layers in HC treatment. This increased value may be attributed to relatively longer time of root growth within 0-20 cm soil layers and resulting longer time for microorganism to growth and utilize root exudates, that were produced the most intensively during root growth in most compacted soli in HC treatment. The increase in soil microbial population with progression of maize growth stages was observed by Li *et al.* (2002), who suggest that root exudates provide C for microbial growth. The average value of DHA in the rhizosphere of heavily compacted soil was more than twice higher than in the bulk soil.

CONCLUSIONS

1. Dehydrogenase activity generally decreases with depth in the bulk soil and in the rhizosphere.

2. Dehydrogenase activity in the rhizosphere was higher than in bulk soil down to the depth of 20 cm irrespective of soil density, and for all depths in heavily compacted soil.

3. The highest differences between bulk soil and the rhizosphere occurred in heavily compacted soil, where soil penetration resistance limited root growth.

4. Dehydrogenase activity in rhizosphere of heavily compacted soil was on average two times higher than in bulk soil, the difference caused probably by increased amount of exudates which helps root to growth in compacted soil and at the same time create favorable environment for soil microorganisms.

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