

Dehydrogenase Activity in a Litter Manipulation Experiment in Temperate Forest Soil

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Abstract – Soil enzyme activities are “sensors” of soil organic matter (SOM) decomposition since they integrate information about microbial status and physico-chemical condition of soils. We measured dehydrogenase enzyme activity in a deciduous temperate oak forest in Hungary under litter manipulation treatments. The Síkfőkút Detritus Input and Removal Treatments (DIRT) Project includes treatments with doubling of leaf litter and woody debris inputs as well as removal of leaf litter and trenching to prevent root inputs. We hypothesized that increased detrital inputs increase labile carbon substrates to soils and would increase enzyme activities particularly that of dehydrogenase, which has been used as an indicator of soil microbial activity. We also hypothesized that enzyme activities would decrease with detritus removal plots and decrease labile carbon inputs to soil. After ten years of treatments, litter removal had a stronger effect on soil dehydrogenase activity than did litter additions. These results showed that in this forest ecosystem the changed litter production affected soil microbial activity: reduced litter production decreased the soil dehydrogenase activity; increased litter production had no significant effect on the enzyme activity.

oak forest / dehydrogenase activity / Síkfőkút Project / litter input / litter removal / soil enzymes

Kivonat – Az avar mennyiségének hatása egy cseres-tölgyes erdő talajában a dehidrogenáz enzim aktivitására. A talajenzimek a talajban lévő szerves anyag (SOM) bomlásának "szenzorai", mivel információt adnak a talaj mikrobiológiai és fizikai-kémiai állapotáról. Egy magyarországi mérsékelt övi tölgyerdőben mértük a dehidrogenáz enzim aktivitását az avar mennyiségének csökkentésével és növelésével. A Síkfőkút DIRT Projectben (Detritus Input and Removal Treatments) az alábbi kezeléseket alkalmaztuk: dupla mennyiségű levél avar, dupla mennyiségű ágavar, valamint levél és gyökér megvonásos kezelések, ahol a gyökereknek a parcellákra történő benövését akadályozzuk meg. Azt feltételeztük, hogy a megnövelt avar input hatására megnövekszik a talajban a labilis, azaz a könnyen bontható szén szubsztrátok mennyisége és az enzimek aktivitása. Különösen a dehidrogenáz enzim aktivitásának változását vártuk, ami az egyik legáltalánosabban használt mutató a talaj mikrobiális aktivitásának mérésére. Továbbá azt feltételeztük, hogy a talaj enzim aktivitása csökkenni fog az avarmegvonásos kezelésekben, a labilis szén szubsztrátok mennyiségének csökkenésével. Eredményeink azt mutatják, hogy tíz év elteltével az avar produkció csökkenése ebben az erdei ökoszisztémában a talaj dehidrogenáz enzim aktivitásának csökkenését okozta, ugyanakkor az avarprodukció növekedése nem okozott szignifikáns változást az enzim aktivitásában.

tölgyerdő / dehidrogenáz aktivitás / Síkfőkút Project / avarmennyiség megduplázása / avarmegvonás / talajenzimek

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1 INTRODUCTION

Soil enzyme activities are “sensors” of soil organic matter (SOM) decomposition since they integrate information about microbial status and physico-chemical condition of soils (Aon – Colaneri 2001, Baum et al. 2003). All soils contain a group of enzymes that determine soil metabolic processes (McLaren 1975) which, in turn, depend on its physical, chemical, microbiological and biochemical properties (Makoi and Ndakidemi 2008). Enzymatic processes are closely related to soil quality, they participate in the processing of unavailable forms of nutrients readily assimilated by plants (Sinsabaugh et al. 1994).

Soil dehydrogenase enzymes (DHA) (EC 1.1.1.1) are one of the main components of soil enzymatic activities participating in and assuring the correct sequence of all the biochemical routes in soil biogeochemical cycles (Ladd 1985). Determination of DHA in soil gives large amount of information about biological characteristic of the soil (Wolińska – Stepniewska 2012). Dehydrogenase enzyme is often used as a measure of any disruption caused by pesticides, trace elements or management practices to the soil, as well as a direct measure of soil microbial activity (Chendrayan et al. 1979; Trevors et al. 1982; McCarthy et al. 1994). Soil DHA is considered to exist in soils as integral parts of intact cells (Taylor et al. 2002). Dehydrogenase enzyme is known to oxidize soil organic matter by transferring protons and electrons from substrates to acceptors (Makoi – Ndakidemi 2008). These processes are part of respiration pathways of soil micro-organisms and are closely related to the type of soil and soil air-water conditions (Kandeler et al. 1996). Several environmental factors, including soil moisture, oxygen availability, oxidation reduction potential, pH, organic matter content, depth of the soil profile, temperature, season of the year, heavy metal contamination and soil fertilization or pesticide use can affect significantly DHA in the soil environment (Dkhar – Mishra 1983; Baruah – Mishra 1984; Sinsabaugh et al. 2008; Xiang et al. 2008; Wolińska – Stepniewska 2012; Kumar et al. 2013).

We measured DHA in a deciduous temperate oak forest in Hungary under litter manipulation treatments. Our research in the Síkfőkút DIRT Project (SIK) constitutes an important part of an international long term project which involves five experimental sites in the USA (H.J. Andrews Experimental Forest, Bousson Experimental Forest, Harvard Forest, University of Michigan Biological Station, Santa Rita) (Nadelhoffer et al. 2004) and one in Germany (Universität Bayreuth BITÖK). We hypothesized that increased detrital inputs would provide increased labile carbon substrates to soils and increase dehydrogenase activities, which is used as indicator of soil microbial activity (Thalmann 1968a; Chendrayan et al. 1979; Nannipieri et al. 2002). We also hypothesized that dehydrogenase activities would decrease in detritus removal plots with decreases in labile carbon inputs to soil.

2 METHODS

2.1 Area and project descriptions

The Síkfőkút Project was established in 1972 for the long-term study of forest ecosystems. It is located in the south part of the Bükk Mountains in North-Eastern Hungary N 47°55' E 20°46' at 325 m altitude. This forest has been protected since 1976, and it is part of the Bükk National Park. Mean annual temperature (MAT) is 10°C and Mean Annual Precipitation (MAP) is 550 mm (Antal et al. 1997). Soil pH ranged between 4.85 and 5.50 depending on the plots (Tóth et al. 2007). Both soil pH and humus content was lower in detritus removal treatments. Humus content ranged between 2.66% and 3.14% (Varga et al. 2008). In the control plots the carbon content was 5.19% (0–5 cm), and 3.25% (5–15 cm) (Tóth et al. 2011). According to the FAO Soil Classification, the soil is a Cambisols. This

forest is a semi-natural stand (*Quercetum petraeae-cerris* community) without forest management activity (Jakucs 1985; Kotrocó et al. 2012). The Síkfókút Project is a member site of the Hungarian LTER Network (Long Term Ecological Research) and the ILTER Network (International Long Term Ecological Research) from 1995 (Kovács-Láng et al. 2000).

Six treatments were established at the Síkfókút DIRT experimental site in the autumn of 2000 each in three replicates on 7×7 m (49 m²) plots. Detritus was not manipulated in the Control plots (CO). There were normal litter inputs in the CO plots. The average leaf-litter production was 3547 kg ha⁻¹year⁻¹ between 2003 and 2010 (Kotrocó et al. 2012). There were two types of detritus additions: double the normal amount of leaf litter was applied to the Double Litter (DL) plots by adding leaf litter removed from NL plots; while in the Double Wood plots (DW) the amount of wood detritus (branches, twigs and bark) was doubled. Annual wood litter amount was measured by boxes placed to the site and its double amount was applied in the case of every DW plots (average 17 kg year⁻¹). In three treatments of detritus removal were also applied: aboveground detritus removed by rake in the No Litter plots (NL), living roots severed by trenching in the No Roots plots (NR), and both NL and NR treatments in No Inputs plots (NI). The NR and NI plots were trenched around 40 cm wide and 100 cm deep. The soil dug out was placed outside the plot. Root-proof Delta MS 500 PE foil was put in the trenches, which was 0.6 mm thick and 1 m wide. Then the trenches were filled with soil. Plants were cleared to eliminate root production (bushes were cut out at the establishment). Weeds were also controlled by Medalon (agent: 480 g l⁻¹ glifosate-ammonium) and dry plant residues were raked. The detailed description of the treatments is in Nadelhoffer et al. (2004), Sulzman et al. (2005), Kotrocó et al. (2008). These processes were replayed every year.

2.2 Soil sampling and measuring of dehydrogenase enzyme activity

Soil samples were collected 11 times from February 2010 to November 2012. Five cores were taken from each plot 15 cm depth with a 2 cm diameter Oakfield soil corer (Oakfield Apparatus Company, USA). Three analytical replicates per sample per assay were used. The samples were homogenized and stored for one week at 4°C.

DHA was determined using the reduction of 2,3,5-triphenyltetrazolium chloride (TTC) method (Thalmann 1968b). Samples of 2 g field-moist soils were mixed with 2 ml 1.5% TTC thoroughly into test tubes. The samples were mixed on a vortex and incubated at 30°C. The control contains only 2 ml Tris buffer (without TTC). After 24 h, the triphenyl formazan, a product from the reduction of TTC, was extracted by adding 10 ml ethanol to each tube and shaken for 1 min. Samples were further incubated at room temperature for 2 h in the dark (shaking the tubes at intervals). The soil suspensions (12 ml) were then filtered and the optical density of the clear supernatant was measured against the blank (ethanol) at 546 nm (red color) at Genesys 10 spectrophotometer. A standard curve was plotted using a range of triphenyl formazan (TPF) (Reanal, Budapest, Hungary) concentrations between 0 and 40 µg TPF ml⁻¹. DHA was expressed as µg TPF g⁻¹ dry soil 24 h⁻¹.

Soil moisture content was measured by TDR 300 (Time Domain Reflectometer) instrument in the field in volumetric water content per cent (vwc%). There were two measurements at each plot at the time of soil sampling to determine DHA. Soil temperature was measured by an ONSET, StowAway TidbiT-type data-logger (Onset Computer Corporation, USA), in the middle of each plot at 10 cm depth. Data-loggers were programmed to measure soil temperature every hour; daily mean of the soil temperature values was used in the paper.

2.3 Statistical analyzes

We used one-way ANOVA to determine significant treatment effects; significant mean differences were evaluated at the level of $p=0.05$ using Tukey's test.

3 RESULTS AND DISCUSSION

We started to measure soil DHA in 2010, ten years after the establishment of treatments. In general, activities were lower in removal treatments (NL, NR, NI) than the control (CO) or addition treatments (DL, DW). Our data show that the dehydrogenase activity is fairly stable in the control plots compared to the treated plots (*Figure 1*). There is a temporal trend in dehydrogenase activity; the effect of detritus removal is increased.

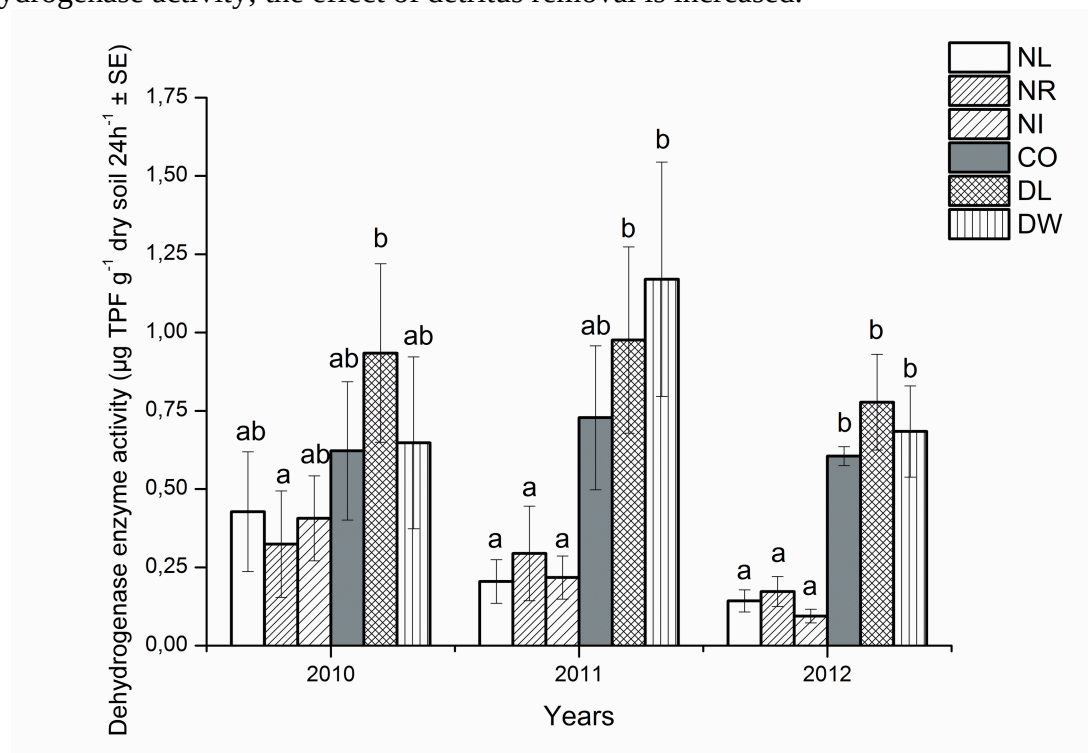


Figure 1. Soil dehydrogenase enzyme activity among treatments between 2010 and 2012 ($\mu\text{g TPF g}^{-1}$ dry soil $24\text{h}^{-1} \pm \text{SE}$). Different letters denote significant treatment differences within each year ($p < 0.05$, ANOVA and Tukey's test).

DHA were significant lower in NR than in DL treatments in 2010 ($p=0.029$). In 2011 there were higher significant differences in dehydrogenase activity among treatments, enzyme activity was higher in DL and DW treatments than in all removal plots ($p < 0.001$). In 2012 litter removal treatments differed significantly not only to DL and DW treatments but also controls ($p < 0.001$) (*Figure 1*). The enzyme activities were higher in DL and DW treatments than controls, but not significantly. In contrast to our initial hypothesis, dehydrogenase activities did not increase significantly with either leaf litter or wood additions. This is generally in agreement with our earlier results for litter decomposition (Fekete et al. 2007), soil respiration (Kotroczó et al. 2008), arylsulphatase and saccharase activities (Fekete et al. 2011). At the other DIRT site in H.J. Andrews Experimental Forest (HJA) in Oregon, Brant et al. (2006a) showed that, soil from the doubled wood treatment had a higher fungal:bacterial ratio, and soil from the no inputs treatment had a lower fungal:bacterial ratio, than the control soil. These changes were the result of alteration in the size and composition of the microbial

community. Brant et al. (2006b) reported microbial biomass values at three DIRT sites: HJA, SIK and BOU (Bousson Experimental Forest in Pennsylvania). They found significant differences in biomass between treatments at SIK. At that site DW plots had a larger biomass than the NR plots and suggestive evidence that the DW plots had a larger biomass than the NI plots. Błońska et al. (2013) report that, DHA is increasing with the diversity of plant communities; this suggest that there is a relationship between the composition of soil organic matter and microbial enzymatic activity. Mamatha et al. (2001) studying soil from red sandy loam areas show that, the DHA is higher in soil covered by plants and in the rhizosphere than non-rhizosphere.

Table 1. Mean values and standard errors of dehydrogenase activity, soil moisture content and soil temperature in terms of the treatments. (Soil moisture and temperature values are the mean values of the days of the measurements). Significant differences in dehydrogenase activity between treatments showed in Figure 1 ($p < 0.05$, ANOVA and Tukey's test).

Treatments	Dehydrogenase activity ($\mu\text{g TPF g}^{-1}$ dry soil $24\text{h}^{-1} \pm \text{SE}$)	Soil moisture ($\text{vwc}\% \pm \text{SE}$)	Soil temperature ($^{\circ}\text{C}$)
2010			
NL	0.43 ± 0.12	34.07 ± 1.95	8.29 ± 4.09
NR	0.32 ± 0.12	41.00 ± 2.01	9.63 ± 4.20
NI	0.41 ± 0.10	38.36 ± 2.02	9.46 ± 4.26
CO	0.62 ± 0.12	34.84 ± 2.63	8.92 ± 3.86
DL	0.93 ± 0.17	34.38 ± 2.56	9.28 ± 3.64
DW	0.65 ± 0.17	35.07 ± 2.99	9.60 ± 4.14
	$p = 0.029$	$p > 0.05$	$p > 0.05$
2011			
NL	0.20 ± 0.08	18.82 ± 3.39	17.69 ± 3.21
NR	0.29 ± 0.11	25.89 ± 4.84	17.93 ± 3.22
NI	0.22 ± 0.08	21.68 ± 4.44	18.02 ± 3.30
CO	0.73 ± 0.13	20.88 ± 4.44	17.86 ± 3.20
DL	0.98 ± 0.20	21.87 ± 4.41	17.13 ± 2.96
DW	1.17 ± 0.23	21.30 ± 4.62	18.07 ± 3.27
	$p < 0.001$	$p > 0.05$	$p > 0.05$
2012			
NL	0.14 ± 0.03	19.93 ± 3.22	12.50 ± 5.68
NR	0.17 ± 0.03	20.66 ± 3.59	12.46 ± 5.75
NI	0.09 ± 0.03	21.32 ± 3.87	12.52 ± 5.76
CO	0.60 ± 0.06	16.18 ± 2.51	12.47 ± 5.76
DL	0.78 ± 0.10	17.36 ± 2.67	12.87 ± 5.34
DW	0.68 ± 0.10	18.26 ± 3.12	12.58 ± 5.75
	$p < 0.001$	$p > 0.05$	$p > 0.05$

We measured the soil moisture and soil temperature at the days when soil sampling was made to determine DHA. We did not find significant treatment differences within each year in soil moisture and in soil temperature (Table 1). The soil moisture values were the highest in 2010 (Figure 2); this year was extremely rainy. Contrarily, years 2011 and 2012 were dry and warm; instead of that the DHA showed same values in the CO plots than in 2010. In the

removal plots DHA decreased in 2011 and 2012. Probably the higher soil moisture caused the higher DHA in 2010. However, we did not find correlation between soil moisture and DHA in years 2010, 2011 and 2012. Kumar et al. (2013) showed significant correlation between DHA and soil moisture. Other authors also attributed the increase in microbial activity in forest soil to higher soil moisture (Görres et al. 1998). Fekete et al. (2011) also found correlation between soil moisture and enzyme activities (arylsulphatase and saccharase) in Síkfőkút between 2004 and 2006. Our results suggest that, changes in soil organic matter content had higher effect on DHA than soil moisture. In other studies also found that more organic matter maintained larger and more active microbial biomass and higher DHA (Chodak et al. 2010; Bonanomi et al. 2011).

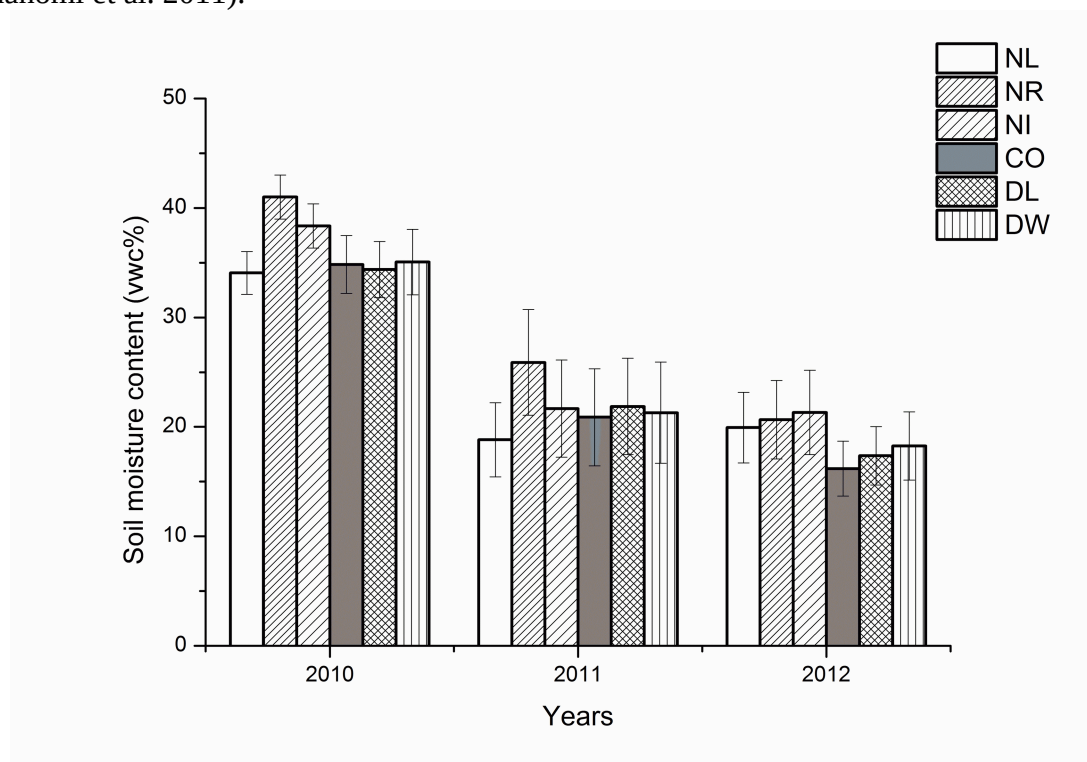


Figure 2. Soil moisture content (vwc%) among treatments between 2010 and 2012.

After ten years of treatments, litter removal had a stronger effect through time on soil dehydrogenase activities than did increase litter inputs. Ectomycorrhizal fungi associated with roots of trees in deciduous forests produce enzymes and thus can increase the surrounding soil enzyme activities (Colpaert – van Laere 2006; Smith – Read 2008). These fungi are responsible for the mobilization of essential plant nutrients by decomposing litter and soil organic materials (Courty et al. 2006). Decomposition of severed roots (NR and NI) would result in the disappearance of mycorrhizal fungi and rhizosphere microbes, causing a considerable reduction in microbial and enzyme activities (Fekete et al. 2011).

4 CONCLUSION

Our findings showed that the changes of litter production significantly affected soil microbial activity, and by extension general nutrient cycling and SOM dynamics in this forest ecosystem. When the litter production decreased, soil dehydrogenase activity also decreased. Increased litter production caused no significant increase in enzyme activity. After ten years of treatments, loss of inputs had a greater impact than increased inputs.

Acknowledgments: We thank Csabáné Koncz for long hours of field and laboratory work. Special thanks are due to Dr. Kate Lajtha and Bruce Caldwell (Oregon State University, Corvallis, USA) and Dr. Kristin Vanderbilt (University of New Mexico, Albuquerque, USA) for their substantial contribution in establishing the experiment. This research was supported by the European Union and the State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP 4.2.4. A/2-11-1-2012-0001 'National Excellence Program'. The work was supported by TÁMOP 4.2.1./B-09/1/KONV-2010-0007, TÁMOP-4.2.2_B-10_1-2010-0024 and TÁMOP-4.2.2.C-11/1/KONV-2012-0010 projects. The TÁMOP projects are implemented through the New Hungary Development Plan, co-financed by the European Social Fund and the European Regional Development Fund.

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