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Impact of temperature on the biological properties of soil

*Agata Borowik and Jadwiga Wyszkowska**

Department of Microbiology, University of Warmia and Mazury in Olsztyn, Plac Łódzki 3, 10-727 Olsztyn, Poland

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A b s t r a c t. The aim of the study was to determine the response of soil microorganisms and enzymes to the temperature of soil. The effect of the temperatures: 5, 10, 15, 20, and 25°C on the biological properties of soil was investigated under laboratory conditions. The study was performed using four different soils differing in their granulometric composition. It was found that 15°C was the optimal temperature for the development of microorganisms in soil. Typically, in the soil, the highest activity of dehydrogenases was observed at 10-15°C, catalase and acid phosphatase – at 15°C, alkaline phosphatase at 20°C, urease and β-glucosidase at 25°C. The highest colony development index for heterotrophic bacteria was recorded in soils incubated at 25°C, while for actinomycetes and fungi at 15°C. The incubation temperature of soil only slightly changed the ecophysiological variety of the investigated groups of microorganisms. Therefore, the observed climate changes might have a limited impact on the soil microbiological activity, because of the high ability of microorganisms to adopt. The response of soil microorganisms and enzymes was more dependent on the soil granulometric composition, organic carbon, and total nitrogen than on its temperature.

K e y w o r d s: soil temperature, microorganisms, ecophysiological biodiversity, enzyme acivity

INTRODUCTION

One of the most important factors determining microbial and biochemical soil activity is temperature. The soil temperature depends on the climate zone, physicochemical properties, and natural topography (Singh *et al*., 2010; Adak and Chakravarty, 2013; Kodaira, 2014). Adak and Chakravarty (2013) demonstrated a strong correlation of soil temperature with air temperature. They indicated a correlation between the surface temperature of the soil and its biological and physical properties.

The amplitude of temperature fluctuations in a soil profile changes periodically, or daily, weekly, monthly, seasonally, and annually. These changes are a function of the climate zone and the depth of a soil profile. This is confirmed by the studies of Licznar and Rojek (2004), according to which, in most Polish soils, the disappearance of daily temperature fluctuations occurs at a depth of 50-60 cm. Michalska and Nidzgorska-Lencewicz (2010) suggested that in a light loam profile, in the area of the Gumieniecka Plain near Szczecin 53°26′17″N 14°32′32″E, the highest average annual temperature reaches 11.6°C and the lowest 7.8°C. This temperature is suitable for psychrophilic microorganisms present in soil. The authors report that the soil temperature is variable at all levels of the soil profile, with the greatest variations relating to the spring period. Licznar and Rojek (2004) have shown that the soil temperature also depends on the moisture content. The temperature amplitudes observed in desiccated soils were larger in comparison to moist soils.

Temperature is one of the main factors that determine the activity of soil microorganisms (Järvan *et al*., 2014). Microorganisms are involved in numerous processes controlling the flow of nutrients through specific enzymes located inside the cell (Borowik *et al*., 2014; Jastrzębska and Kucharski, 2007; Wyszkowska *et al*., 2013), and their activity is dependent, among others, on the temperature. Järvan *et al*. (2014) suggest that temperature is one of the most important factors influencing the count and occurrence of microorganisms and is also a determinant of the activity of intracellular and extracellular enzymes. The temperature of the soil affects the stability and resistance

*Corresponding author e-mail: jadwiga.wyszkowska@uwm.edu.pl

of microorganisms (D'Amico *et al*., 2006) as well as their activity, regardless of their feeding type. It is a factor that limits the activity of both heterotrophic and litotrophic microorganisms (Zeppel *et al*., 2012).

It is widely assumed that soil microorganisms are mesophilic microorganisms. However, this view may be not valid in all climate zones. In the case of Polish soils, it should rather be recognized that the most active are psychrophilic microorganisms, although the important role of mesophilic microorganisms, whose survival varies over a fairly wide range of temperatures, cannot be excluded. According to Tortora *et al*. (2004), the optimum temperature for growth of psychrophilic bacteria is between 15 to 20°C and for mesophilic bacteria from 20 to 40°C. With the above-mentioned data in mind, it is extremely important to determine a correlation between the soil temperature and microbial activity. Therefore, the aim of this study was to determine the relationship between soil temperature and the growth and development of microorganisms, their diversity, and activity of soil enzymes.

MATERIALS AND METHODS

In the laboratory experiment, the soil material collected from the arable humus level of typical brown earths (Eutric Cambisol) originated from the Experimental Teaching Centre in Tomaszkowo (north-eastern Poland, 53.7167 °N, 20.4167 °E). According to the classification of grain size by the United States Department of Agriculture, the soil was characterized by the following granulometric composition: sand (S), loamy sand (LS), sandy loam (SL), and silty loam (SiL). The properties of the soil are shown in Table 1. The soils used in the experiment were passed through a sieve with a mesh size of 2 mm.

The study was conducted under laboratory conditions. The soils (S, LS, SL, or SiL) in an amount of 100 g d.m. were placed in glass beakers with a capacity of 150 cm^3. Soil moisture content was adjusted to 60% of capillary water capacity using sterile distilled water. The beakers were covered with perforated foil, and the soil was incubated for 16 weeks in incubators at 5, 10, 15, 20, or 25°C. In the 4th and 16th week, the experiment was partially liquidated and microbiological and biochemical properties were determined in the samples of the soils mixed in the beakers. Water loss was supplemented once a week. The experiment was conducted in 3 replicates for each period. The total number of beakers for each soil was 30.

The count of soil microorganisms in the individual soil samples collected from each beaker was determined using a plate count method in 5 replicates. The count of heterotrophic bacteria, colonies of *Azotobacter*, actinomycetes, and fungi was determined on the media characterized by Kucharski and Wyszkowska (2004). Microorganisms were cultured at 28°C. The grown colonies of the *Azotobacter* were counted after 2 days, those of heterotrophic bacteria and actinomycetes after 7 days, and those of fungi after 5 days. In order to determine the colony development index (CD) of microorganisms and their ecophysiological diversity index (EP), the cultures of appropriate solutions with a medium were counted daily for 10 consecutive days. The colony development index $CD = [N_1/1 + N_2/2 + N_3/3\ldots..$

T a b l e 1. Physicochemical properties of the soil

Soil properties		Soil type			
		Sand	Loamy sand	Sandy loam	Silty loam
Percentage of fraction (d)	2.00 ≥ d > 0.05 mm	92.47	85.18	51.27	34.96
	0.05 ≥ d > 0.002 mm	7.07	13.82	45.36	60.21
	d ≤ 0.002 mm	0.46	1.00	3.37	4.83
pH_{KCl}		6.6	6.3	6.8	7.0
HAC		6.5	14.4	5.2	6.5
EBC	mM(+) kg^{-1} of soil d.m.	35.5	49.2	131.4	197.2
CEC		42.0	63.6	136.6	203.7
BS	%	84.5	77.3	96.2	96.8
C_{org}	g kg^{-1} of soil d.m.	3.9	6.7	9.9	9.9
N_c		0.03	0.61	1.14	1.38
K_w	mg kg^{-1} of soil d.m.	66	168	168	196
Na_w		41	46	57	53
Ca_w		599	812	2214	3556
Mg_w		26	28	50	74

HAC – hydrolytic acidity, EBC – sum of exchangeable cations, CEC – cation exchange capacity, BS – base saturation; C_{org} – organic carbon, c – total, w – replaceable.

N_{10}/10] 100, where N_1, N_2, N_3,…. N_{10} is a proportional count of colonies grown in (Sarathchandra *et al*., 1997), and the ecophysiological diversity index EP = -∑(pi log pi), where pi is the number of microbial colonies from a given day divided by the total number of colonies (De Leij *et al*., 1993), were then calculated.

Enzyme activity, similarly to the microbial count, was determined in the individual soil samples. The measurements were performed in each sample in 3 replicates. Dehydrogenase activity (EC 1.1) was determined using the Lenhard method modified by Öhlinger (1996), while catalase (EC 1.11.1.6), urease (EC 3.5.1.5), arylsulfatase (EC 3.1.6.1), β-glucosidase (EC 3.2.1.21), acid photsphatase (EC 3.1.3.2), and alkaline phosphatase activities (EC 3.1.3.1) were determined according to Alef *et al*. (1998).

The following substrates for the enzymes were used: 2,3,5-triphenyltetrazolium chloride (TTC) for dehydrogenases, hydrogen peroxide for catalase, disodium 4-nitrophenylphosphate (PNPNa) for phosphatases, urea for urease, p-nitrophenyl-β-D-glucopyranoside (PNG) for β-glucosidase, and potassium 4-nitrophenylsulfate (PNS) for arylsulfatase. Enzyme activity was expressed per 1 kg of soil d.m. h^{-1} in the following units: μM of triphenylformazan (TPF) for dehydrogenases, M of O_2 for catalase, mM of N-NH_4 for urease, and mM of p-nitrophenol (PNP) for acid phosphatase, alkaline phosphatase, β-glucosidase, and arylsulfatase. All enzyme activity assays, except for catalase, were performed using a Perkin-Elmer Lambda 25 (Massahusets, USA) spectrophotometer.

Prior to the experiment, the granulometric composition of the soil samples was determined using a laser particle size analyser Mastersizer 2000; their pH was determined by a potentiometric method in an aqueous solution of KCl at a concentration of 1 M dm^3; hydrolytic acidity (HAC) and sum of exchangeable cations (EBC) – by the Kappen method (Carter, 1993), content of total nitrogen according to the method by Kjeldahl, and the content of bioavailable phosphorus, potassium, calcium, and magnesium according to the Atomic Absorption Spectrometry (ASA) method; organic carbon (C_{org}) content – by the Tiurin method (Nelson and Sommers, 1996). Based on the HAC and EBC values, cation exchange capacity (CEC) and the degree of soil saturation with basic elements (BS) were calculated. The following formulas were used: CEC = EBC + HAC; BS = (EBC/CEC) 100.

The analysis of ANOVA variance for the results was performed using the Statistica 10.0 (StatSoft, 2012) package. Homogenous groups were calculated with Tukey test, at p = 0.01. Simple Pearson correlation coefficients were calculated for dependent and independent variables. The results were also analyzed using the PCA test (principal component analysis). Moreover, analysis of variance ANOVA was used to calculate the η^2 coefficient, which specifies the contribution of each independent variable to the formation of dependent variables.

In this study, the results of biological and biochemical analyses were presented as the means from two periods, because the analysis of η^2 coefficients showed that the soil incubation time did not significantly affect the count of microorganisms, their diversity, and enzyme activity.

RESULTS

The studies demonstrate that the temperature, regardless of the type of soil formation, significantly shapes the conditions for growth and development of microorganisms (Table 2). Heterotrophic bacteria, *Azotobacter*, actinomycetes, and fungi proliferated the most intensively in the soils incubated at 15°C. At this temperature, their count was from 29% (actinomycetes) to 67% (*Azotobacter*) higher in comparison to the soils at 5°C, and from 23% (fungi) to 42% (heterotrophic bacteria) higher in comparison to the soils incubated at 25°C.

The PCA analysis clearly indicates that the best temperature for soil microorganisms is 15°C, while the least favourable temperatures are 5 and 25°C (Fig. 1). The microbiological properties of individual soil formations differed

T a b l e 2. Impact of temperature on the count of soil microorganisms

Temperature (ºC)	Microorganisms			
	Org x10^9	Az x10^3	Act x10^9	Fun x10^7
	10^n cfu kg^{-1} soil d.m.			
5	15.14c	6.50c	7.55c	32.16d
10	18.68b	8.29b	8.57b	39.50b
15	20.61a	10.84a	9.67a	42.99a
20	14.71c	9.28ab	7.50c	36.71c
25	12.25d	8.14b	5.56d	32.96d
	Coefficient of correlation			
	-0.46	0.42	-0.53*	-0.04

Org – organotrophic bacteria, Az – *Azotobacter*, Act – actinomycetes, Fun – fungi; the same letters in the columns indicate homogeneous groups; *correlation significant at p ≤ 0.01 between temperature and count of microorganisms n = 23.

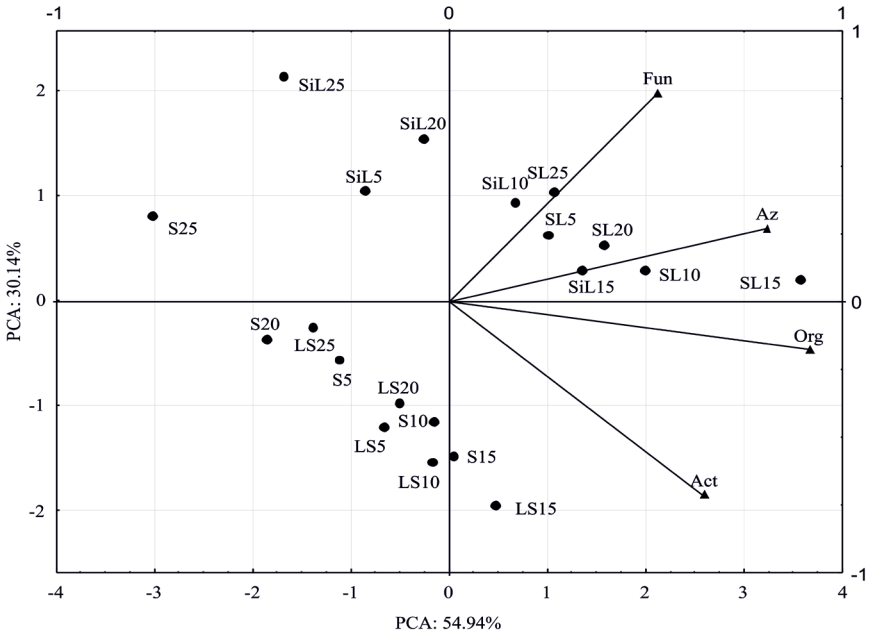

Fig. 1. Impact of temperature on the count of soil microorganisms. Org – heterotrophic bacteria, Az – *Azotobacter*, Act – actinomycetes, Fun – fungi; S – sand, LS – loamy sand, SL – sandy loam, SiL – silty loam; temperature: 5, 10, 15, 20, 25°C.

T a b l e 3. Impact of temperature on the colony development and the ecophysiological diversity indexes of microorganisms

Temperature (°C)	Index					
	Colony development			Ecophysiological diversity		
	Microorganisms					
	Org	Act	Fun	Org	Act	Fun
5	34.48c	23.97d	36.43c	0.87a	0.90b	0.73c
10	34.45c	25.37b	36.19c	0.86ab	0.90b	0.77a
15	34.55c	26.12a	39.70a	0.87a	0.92a	0.77a
20	35.56b	24.54c	37.42b	0.85b	0.90b	0.75b
25	36.25a	25.05bc	36.58 c	0.82c	0.90b	0.71d
			Coefficient of correlation			
	0.90*	-0.14	0.66*	-0.90*	0.23	0.41

*Explanation as in Table 2.

significantly. The highest counts of microorganisms were observed in sandy loam, lower in silty loam, and the lowest in sand. The most favourable temperature was 15°C, and the least favourable temperatures were 25 and 5°C, although in some soil formations, the temperature preferences were different. For example, the development of heterotrophic bacteria in sand, loamy sand, and silty loam were similar at 10 and 15°C, while in sandy loam at 20°C. A soil temperature of 25°C resulted in a reduction of actinomycete count in silty loam, sand, and loamy sand in comparison to 5°C. The count of these microorganisms was similar only for sandy loam incubated at 5 and 25°C. The highest counts of fungi were achieved during soil incubation at the above-mentioned temperature of 15°C. At this temperature, the count of fungi in sand, sandy loam, and silty loam was higher than at 5°C.

The studied temperature range (5-25°C) slightly changed the diversity of microorganisms (Table 3). The colony development index ranged: from 34.48 to 36.25 (incubation temperature 5 and 25°C) for heterotrophic bacteria, from 23.97 to 26.12 (incubation temperature 5 and 15°C) for actinomycetes, and from 36.43 to 39.70 (incubation temperature 5 and 15°C) for fungi.

Soil temperature had an ambiguous effect on the value of the ecophysiological diversity index (EP). The highest EP values were found in fungi isolated from the soil at

T a b l e 4. Impact of temperature on the activity of soil enzyme

Temperature (°C)	Enzymes						
	Deh	Cat	Ure	β-glu	Pac	Pal	Aryl
	µM TFF	M O_2	mM N-NH_4	mM PNP			
	kg^{-1} soil d.m. h^{-1}						
5	10.98b	0.28ab	1.30e	0.52c	1.08d	1.59e	0.22a
10	11.47a	0.29b	1.40d	0.40d	1.14c	1.64d	0.23a
15	11.24ab	0.31a	1.52c	0.58b	1.20a	1.68c	0.23a
20	9.83c	0.27c	1.67b	0.59b	1.17b	1.82a	0.21ab
25	9.15d	0.25d	1.78a	0.61a	1.14c	1.79b	0.17c
	Coefficient of correlation						
	-0.84*	-0.59*	0.99*	0.69*	0.56*	0.93*	-0.76*

Deh – dehydrogenases, Cat – catalase, Ure – urease, Pac – acid phosphatase, Pal – alkaline phosphatase, Glu – β-glucosidase, Aryl – arylsulfatase. Other explanation as in Table 2.

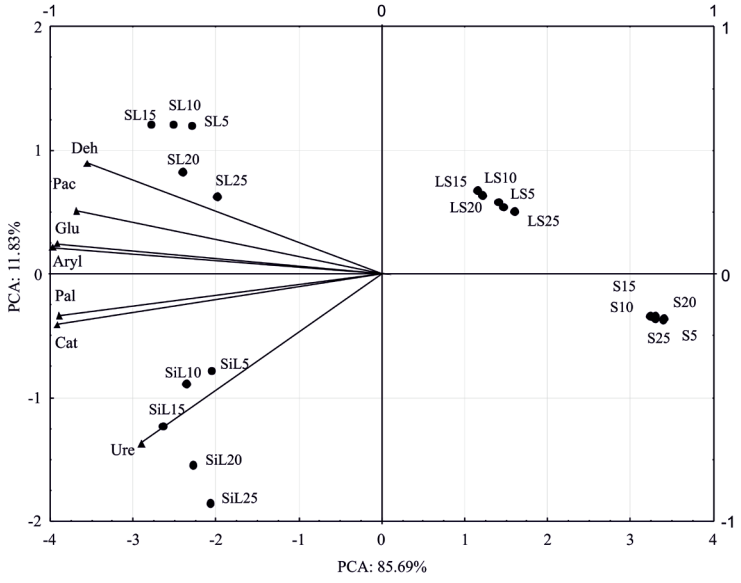

Fig. 2. Activity of soil enzymes in soils with different temperatures (PCA). Deh – the activity of dehydrogenases, Ure – urease, Pac – acid phosphatase, Pal – alkaline phosphatase, Glu – β-glucosidase, Aryl – arylsulfatase, Cat – catalase.S – sand, LS – loamy sand, SL – sandy loam, SiL – silty loam; temperature: 5, 10, 15, 20, 25°C.

a temperature of 10°C and 15°C (Table 3). In turn, the EP of actinomycetes depended on the temperature within a very limited scope. The mean results obtained for all the soil formations indicate a certain trend of a favourable influence of 15°C on the ecophysiological diversity of these microorganisms. The EP index value of heterotrophic bacteria isolated from the soils incubated in the temperature range of 5-15°C was almost the same, while higher temperatures decreased the EP value by a few per cent.

In the presented study, soil incubation temperature also had a significant impact on the activity of soil enzymes (Table 4). The activity of urease and β-glucosidase was the highest in the soils incubated at 25°C, but and that of alkaline phosphatase – at 20°C, regardless of the type of soil formation. The activity of these enzymes was from 17% (β-glucosidase) to 37% (urease) higher than at 5°C. In turn, the activity of dehydrogenases was the highest in the soil samples at 10-15°C, while the activity of catalase and acid phosphatase – at 15°C, as in the case of the bacterial count.

Figure 2 shows the dispersion of enzymes in the system of the two first principal components. The horizontal axis explains 85.69% of the total variance of the variables, while the vertical axis 11.83%. Vectors representing primary variables of all the studied enzymes focused around the axis representing the first variable principal component. They are characterized by a high negative fitting. The activity of all the enzymes had a highly significant positive correlation. However, no correlation between the activity

of dehydrogenases and urease was found. The projection of cases on the plane with factors indicated that the highest enzyme activity was observed in sandy loam and silty loam, while the activity in loamy sand and sand was lower. Analysis of the distribution of individual cases representing enzymatic activity shows that the type of soil formation differentiated enzyme activity in a more significant way than the temperature.

DISCUSSION

Similarly to air temperature, soil temperature has a huge impact on the biology of the soil. According to Feng and Simpson (2009), the diversity of microorganisms changes in the soil within a temperature range from 2 to 20°C. It is very important in the climate change context. Based on own research, it was demonstrated that microorganisms can adapt to low temperatures, which was confirmed by the fact that the optimal temperature for their development was 15°C. At this point, it is worth mentioning that in Poland the average soil temperature ranges from 9 to 10°C (Michalska and Nidzgorska-Lencewicz, 2010). The 10-year study of Nieróbca (2005) shows that in a layer of 5 cm to 20 cm, the average annual temperature of soil equals 9.4°C, while the average value for the warmest months *ie* from June to September is only 16°C. The latter is close to the average temperature, which has the most favourable effect on the proliferation of microorganisms in the present study.

A temperature decrease affects microorganisms in both ways: indirect and direct. The indirect action involves a reduction in the production capacity of plants and the resulting consequences for the microorganisms, while the direct action results from the adverse effect on the metabolism of microorganisms (Jefferies *et al*., 2010). Vorboyova *et al*. (1996) found that a long-term impact of low temperatures causes adaptation of microorganisms, which is reflected in the change of microbial metabolism and enzyme activity. Psychrophilic organisms are able to adapt to low temperatures (D'Amico *et al*., 2006), which enables their growth and development in various climatic zones.

The study of Jefferies *et al*. (2010) suggests that substrates released by plants and microbial cells in the autumn and winter can limit the growth of microorganisms, while an increase in temperature may increase the growth of psychrophilic microorganisms. As a result, a reduction in the bacterial biomass in late winter can be observed. This number of microbial cells results in activating nutrients necessary for plant growth in the early spring.

The soil temperature significantly influences the structure of microorganisms and their functionality. The conducted studies show that the highest colony development index (CD) of heterotrophic bacteria was recorded in soils incubated at 25°C, while for actinomycetes and fungi it had its highest value at 15°C. The soil temperature slightly changed the ecophysiological diversity of the studied groups of microorganisms. In turn, Papatheodorou *et al*. (2004) claim that bacterial diversity is greater in soils at higher temperatures. An increase in soil temperature may lead to changes in bacterial protein profiles, kinetic parameters related to breathing, and the decomposition rate of organic matter in the soil (Jezierska-Tys and Frąc 2008; Wyszkowska *et al*., 2013). Both own research and literature (Papatheodorou *et al*., 2004) indicate that bacterial diversity is limited by low temperatures.

The effect of temperature on enzyme activity is not a simple dependence. Biochemical activity, as well as microbial activity, is modified by the changing temperature of the soil (Jefferies *et al*., 2010; Papatheodorou *et al*., 2004; Vorboyova *et al*., 1996). Own research indicates that it is not possible to assume a constant temperature, because a stable temperature does not exist in the environment. Typically, the highest activity in the soil is recorded at 10-15°C for dehydrogenases, at 15°C for catalase and acid phosphatase, at 20°C for alkaline phosphatase, and at 25°C for urease and β-glucosidase. The optimum temperature for individual enzymes is a function of an increased reaction rate related to an increase in kinetic energy, and an increased rate of thermal denaturation of the enzyme above its critical (60 °C) temperature (Acosta-Marinez and Tabatabai, 2002). It has to be remembered that in the case of own research the soil incubation temperature was different (from 5 to 25°C), which is significantly below the critical temperature. Therefore, in our research the thermal denaturation of enzymes did not accrue. Davidson and Janssens (2006) and Wallenstein *et al*. (2010) also observed variable activity of soil enzymes depending on the soil temperature. Enzyme activity increased during thaw and decreased with the onset of winter. The studies of these authors show that biochemical processes are much more intense under the conditions of variable temperature, which happens in the soil environment. A consequence of climate changes could be the limited availability of substrates to both intracellular and extracellular enzymes (Borowik *et al*., 2014; Davidson and Janssens, 2006; Kodaira, 2014; Singh *et al*., 2010). Acosta-Marinez and Tabatabai (2002) showed that arylamidase activity increased with a temperature increase from 20 to 60°C. Higher temperature caused denaturation of this enzyme. According to D'Amico *et al.* (2006), psychrophiles produce cold-adapted enzymes that have high specific activities at low temperatures, significantly higher than those observed for their mesophilic counterparts.

In our research, the enzymatic activity was significantly positively correlated with the count of *Azotobacter* bacteria and fungi, for which the best proliferation conditions were in the soils at 15°C. According to D'Amico *et al*. (2006), this results from the fact that the activity of psychrophilic microorganisms is often an order of magnitude higher in comparison to that of mesophiles.

According to Michalska and Nidzgorska-Lencewicz (2010), the average annual temperature of the soil is approx. 9-10°C. Thus, the adaptation of microorganisms to this temperature was the most possible. The number of microorganisms was positively correlated with the richness of soil with nutrients and the content of organic carbon (Davidson

and Janssens, 2006; Jefferies *et al*., 2010). In our research, organic carbon, total nitrogen, and bioavailable phosphorus, potassium, calcium, and magnesium content probably determined the positive correlation between the activity of soil dehydrogenases, catalase, urease, acid phosphatase, alkaline phosphatase, β-glucosidase, and arylsulfatase and the content of colloidal clay and silt fractions.

CONCLUSIONS

1. The most favourable temperature for the development of soil heterotrophic bacteria, *Azotobacter*, fungi, and actinomycetes was 15°C. Typically, in the soil, the highest activity of dehydrogenases was observed at 10-15°C, catalase and acid phosphatase at 15°C, alkaline phosphatase at 20°C, and urease and β-glucosidase at 25°C.

2. The highest colony development index for heterotrophic bacteria was observed in the soils incubated at 25°C, while for actinomycetes and fungi at 15°C. The incubation temperature of the soil only slightly changed the ecophysiological diversity of the studied groups of microorganisms.

3. The response of soil microorganisms and enzymes was more dependent on the granulometric composition, organic carbon, and total nitrogen of the soil than on its temperature.

4. The observed climate changes might have a limited impact on the soil microbiological activity, because of the high ability of microorganisms to adopt.

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