

EDAPHIC FACTORS AND THEIR INFLUENCE ON THE MICROBIOLOGICAL BIODIVERSITY OF THE SOIL ENVIRONMENT

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Abstract: The edaphic factors are the soil properties that affect the diversity of organisms living in the soil environment. These include soil structure, temperature, pH, and salinity. Some of them are influenced by man, but most are independent of human activity. These factors influence the species composition of soil microbial communities, but also their activity and functionality. The correlations between different abiotic factors and microbial groups described in this manuscript indicate both the complexity of the soil environment and its sensitivity to various stimuli.

1. Introduction. 2. Soil type and structure. 3. Soil pH and salinity. 4. Soil temperature. 5. Soil moisture. 6. Organic carbon and nitrogen content. 7. Heavy metals content. 8. Conclusions

CZYNNIKI EDAFICZNE I ICH WPŁYW NA BIORÓŻNORODNOŚĆ MIKROBIOLOGICZNĄ ŚRODOWISKA GLEBOWEGO

Streszczenie: Czynniki edaficzne to właściwości gleby, które wpływają na różnorodność wszystkich organizmów żyjących w środowisku glebowym. Należą do nich m.in. struktura gleby, temperatura, pH, zakwaszenie i zasolenie. Na niektóre z nich człowiek ma wpływ, ale większość z nich jest niezależna od działalności człowieka. Czynniki te, wpływają na skład gatunkowy zbiorowisk mikroorganizmów glebowych, ale także na ich aktywność oraz funkcjonalność. Opisane w niniejszym manuskrypcie korelacje pomiędzy różnymi czynnikami abiotycznymi oraz grupami drobnoustrojów wskazują zarówno na złożoność środowiska glebowego, jak i jego wrażliwość na różne bodźce.

1. Wprowadzenie. 2. Typ i struktura gleby. 3. pH i zasolenie gleby. 4. Temperatura gleby. 5. Wilgotność gleby. 6. Zawartość węgla organicznego i azotu. 7. Zawartość metali ciężkich. 8. Podsumowanie.

Key words: abiotic factors, biodiversity, edaphic factors, soil functionality, soil microorganisms

Słowa kluczowe: czynniki abiotyczne, bioróżnorodność, czynniki edaficzne, funkcjonalność gleby, mikroorganizmy glebowe

1. Introduction

Soil microbiome includes all saprophytic microorganisms, commensals and parasites that inhabit the soil. It is estimated that one gram of fresh fertile soil matter can contain up to billions of bacteria [53]. The taxonomic and functional diversity of microorganisms and their interactions affect the functioning of the whole soil ecosystem. Many species complement each other and form a system responsible for soil processes. The functional diversity of soil microbiomes is related to the proper functioning of terrestrial ecosystems. The diversity of microorganisms in the soil environment depends on the physical and chemical properties of the soil and, indirectly, on the anthropogenic factors that influence them.

Ecological (environmental) factors are divided into abiotic and biotic. This study is concerned with abiotic factors, *i.e.* inanimate elements of the environment, which affect the functioning of living organisms

directly or indirectly. They are chemical and physical parts of the environment. The whole range of soil conditions affecting the life of soil organisms is called edaphic factors. They are distinguished as a separate group of abiotic factors according to the importance of soil in terrestrial ecosystems. They are prerequisites for the existence of specific habitat conditions and, as a result of the specific composition of the community of the organisms that inhabit them [35].

Among the edaphic factors related to the soil we can distinguish (Fig. 1.):

- soil structure and type,
- soil temperature,
- soil moisture,
- soil pH and acidity,
- mineral salt content (salinity).

Shelford's universal ecological law says that the optimal development of any organism depends on the balance of a complex of environmental factors [36]. The ecological tolerance is a range of any factor (abiotic

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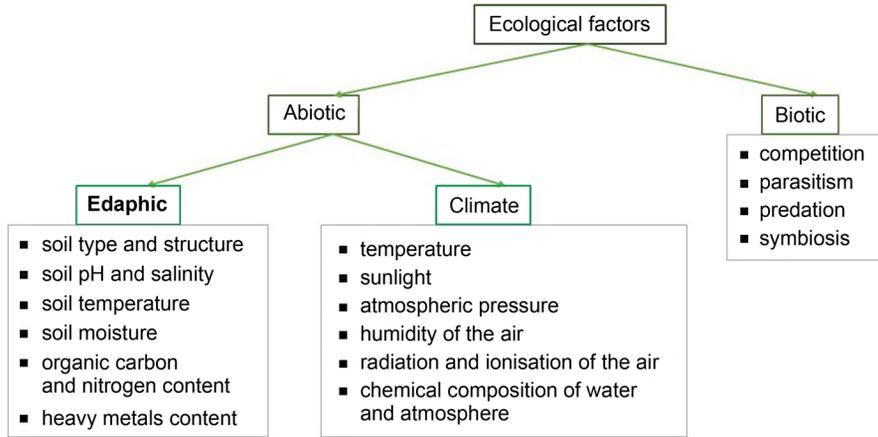


Fig. 1. Types of ecological factors.

or biotic) in which the organism can exist, *i.e.* perform physiological processes. However, the maximum growth, activity and reproduction of each organism take place within the limits of the optimum occurrence of a given environmental factor (Fig. 2). This also applies to soil microorganisms.

The availability of water, temperature and salinity vary the types of soil microorganisms and create frontiers, in which the microorganism can survive and affect competition between species. Edaphic properties are the basic ecological filter affecting the structure of soil microbiomes [9].

Many previous studies of microorganisms based on microbiological cultures on a specific medium, which eliminated a large part of microorganisms that are defined as an uncultured [51]. However, it is now known that only 1% of soil microorganisms can be

isolated using traditional methods [15]. For this reason, modern techniques, including molecular biology, are increasingly present in soil microbiology research. In recent years metagenomics has developed. It is a method of genome analysis consisting of all microorganisms inhabiting the environment [76]. Modern research methods allow us to explore the influence of various environmental factors on soil microorganisms [18]. Researchers use them to analyze the impact of the environment on the diversity of soil microorganisms. Some research concerning the influence of edaphic factors on soil microbiome is presented in this review.

The aim of this review is to determine the existing knowledge on the most important abiotic factors influencing soil microorganisms and to highlight the importance of modern research methods in the identification of soil microbiological biodiversity.

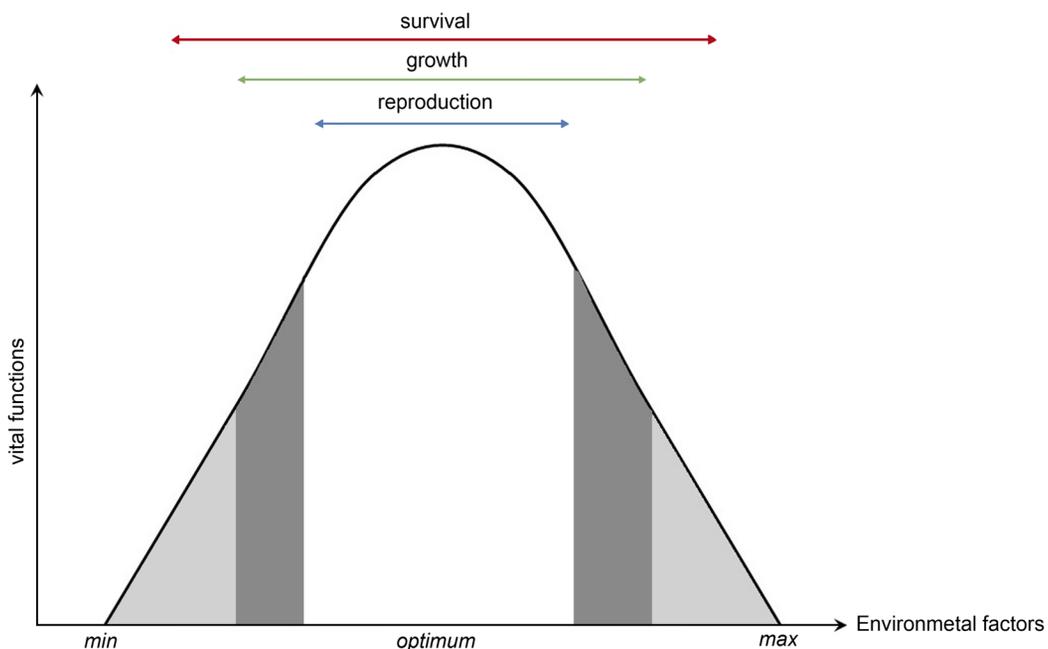


Fig. 2. General ecological tolerance curve of the species. Based on Lynch and Gabriel [45].

2. Soil type and structure

Soil structure includes the size, shape, and arrangement of particles such as sand, silt, and clay [39]. It was shown that micro-grained soils usually contain higher amounts of microbial biomass than coarse-grained soils. It was found that the lighter soil structure favoured the development of bacteria [4]. Researchers indicate that clay molecules and a higher number of micropores in fine-grained soil limit the development of mesofauna, which protects microorganisms from predation [50]. Meliani *et al.* [50] showed that bacterial abundance was correlated with soil fractions, while no correlation between fungal abundance and fractions was observed. Using Terminal-Restriction Fragment Length Polymorphism (T-RFLP) analysis researchers found dominant associations of *Alphaproteobacteria* to large soil particles (*i.e.* sand) and *Halophaga* and *Acidobacterium* associations with smaller soil's particles (*i.e.* clay) [66].

With the use of classical microbiological methods, *i.e.* culture on media, the research on 18 soil types in Georgia showed that soils differ in their total bacterial abundance and in the prevalence of some types of bacteria such as *Bacillus*, *Pseudomonas* and *Rhodococcus* [17]. It was found that brown, chernozem and marshy soils are the richest in terms of bacterial abundance. *Bacillus* bacteria dominate in the majority of soils studied by researchers, *Pseudomonas* bacteria were the most abundant in alluvial and brown forest soils, while *Rhodococcus* sp. is common in yellow-brown and red forest soils. In the course of research conducted on eight types of Polish soils by Grządziel and Gałązka [26] using the next generation sequencing (NGS; MiSeq, Illumina), a ten types of bacteria common to all eight soils were selected: *Conexibacter*, *Bacillus*, *Saccharopolyspora*, *Rhodoplanes*, *Azospirillum*, *Paenibacillus*, *Streptomyces*, *Gemmatimonas* and *Mycobacterium*. The analysis of the microbiome of the chickpeas rhizosphere growing on different soil types in the same climate also showed that microbiomes differ from soil to soil [47]. This eubacterial community structure was examined by denaturing gradient gel electrophoresis (DGGE), and the authors have concluded that the bacterial community structure in the rhizosphere as affected by a complex interaction between soil type and plant species. In different soil types under lettuce cultivation subjected to the same agrotechnical treatments and identical climatic conditions, bacterial differentiation depending on the soil type was found [65]. Kuramae *et al.* [38] using the PhyloChip analysis, which is the high-density DNA microarray, also indicate that some bacterial taxa are strongly correlated with the physicochemical properties of the soil.

The determination of an unequivocal influence of soil type and type on the structure of microbial com-

munities is a difficult issue because of the complexity of taking into account many variables (minerals, texture, pH, physical structure, *etc.*) when comparing different soils.

3. Soil pH and salinity

The soil pH depends on the type of rock from which the soil was formed. Acid soils are formed from igneous rocks and sands. Alkaline soils are formed from carbonate rocks (*e.g.* limestone). In addition, the pH of the soil is influenced by climate, rock weathering, organic matter and human activity [21]. The soils are strongly acidic ($\text{pH}_{\text{KCL}} < 4.5$), acidic ($\text{pH}_{\text{KCL}} 4.5 - 5.5$), slightly acidic ($\text{pH}_{\text{KCL}} 5.6 - 6.5$), neutral ($\text{pH}_{\text{KCL}} 6.6 - 7.2$) and alkaline ($\text{pH}_{\text{KCL}} > 7.2$) [23]. In Poland, the soil pH ranges from 3.0 to 8.5. The lowest pH is found in non-carbonate forest soils and the highest in carbonate soils [23].

The impact of various factors on the composition of soil microorganisms was investigated using 16S V4–5 region sequencing (HiSeq, Illumina) and it was shown that soil pH has a significant influence on the development of specific bacteria [57]. Researchers showed, that soil pH significantly correlated with such bacteria phyla as *Acidobacteria*, *Beta-Proteobacteria* and *Bacteroidetes*. In another study, using NGS, it was also shown that the pH is often identified as the main factor affecting, in particular, the bacterial communities and archaea [9]. Different groups of microorganisms have distinct limits for optimal pH, so that acidic, neutral and alkaline soils have a different microbial structure, both in terms of quantity and diversity of the population. The pH value indirectly affects the structure of microbial communities, also by influencing the availability of nutrients in the soil [57]. Most soil microorganisms prefer a pH close to neutral (6–7). However, there are also those adapted to extreme pH values, *i.e.* acidophiles and alkalophiles. Acidophilic microorganisms develop in very acidic environments at pH 3.0 or lower. These are, among others, bacteria from genera: *Acidithiobacillus*, *Thiobacillus*, *Acetobacter*, *Alicyclobacillus* and some species from the *Acidobacteria*. Archaea representatives were isolated from dry soil (Japan) with extremely low pH: *Picrophilus torridus* and *P. oshimae*, which develop at pH 0.7 [59]. Alkalophiles grow optimally at pH above 9.0, which is found in desert sodium soils (*e.g.* in the west of the United States). Among the alkalophilic microorganisms present in the soil one can distinguish the representatives of the genera *Bacillus*, *Flavobacterium*, *Methanobacterium*, and *Corynebacterium*. Extreme alkalophilic actinomycete strain isolated from desert soil in Egypt consistently to the genus *Nocardopsis*, which was confirmed by 16S rDNA analysis and researchers

proposed name *N. alkaliphila*. This bacterium grows at pH between 7.0 and 12.0 [30].

Analysis of soil Phospholipid Fatty Acid (PLFA) showed that low pH can increase the total abundance of fungi in the soil fivefold, with a simultaneous decrease in the number of bacteria [62]. They are preferable to pH between 4 and 6, and some of them, such as *Saccharomyces*, *Aspergillus*, *Penicillium* or *Trichosporon*, are even acidophilic [34]. Grządziel and Gałązka [26] showed that the soil with the lowest pH analyzed (4.0; Brunic Arenosol I) was characterized by a different microbiome than the other seven soil types. In the Dutch soils, a strong correlation was found between the number of *Bacilli* and *Clostridium* groups with soil pH and phosphorus content [38]. The metagenomic DNAs from soil bacteria analysed by pyrosequenced revealed that in acidic soils (≤ 6.5) a higher diversity and the total number of bacteria was observed in comparison with soils with neutral pH (7.7) [6]. The T-RFLP analyses of soil samples from North and South America also showed that pH is a very important factor influencing the diversity and abundance of soil microorganisms. However, the researchers noted a lower bacterial diversity in acidic soils compared to neutral soils [14]. The effect of pH on the microbial community is already noticeable at broad levels of taxonomic resolution. Zhang *et al.* [81] using high-throughput sequencing observed that the abundance of actinobacteria, *Bacteroidetes*, *Fibrobacteres* and *Firmicutes* was higher at close to neutral pH and much lower at acidic and alkaline pH. *Acidobacteria*, *Chloroflexi* and *Planctomycetes* bacteria were abundant in acidic pH soil, then in neutral pH their number decreased and in alkaline pH slightly increased. The number of bacteria from the genera *Gemmatimonadetes*, and *Nitrospirae* [81] increased linearly with the increase in pH of the soil. One of the most pH-sensitive processes in the soil is nitrification. The conversion of ammonium ions (NH_4^+) to nitrates (NO_3^-) is dependent on the alkalophilic bacteria *Nitrobacter* and *Nitrosomonas*, which optimally increase at pH 7.6–8.8 and are very sensitive to changes in pH [34]. At the same time, the nitrification process affects the pH of the soil, as, during the uptake of NH_4^+ ions by microorganisms, the environment becomes acidified, and during the uptake of NO_3^- ions by bacteria, the soil becomes alkaline [34]. The balance between the two stages of the nitrification reaction allows a constant pH of the soil to be maintained.

In addition to the soil reaction, the salinity level is very important for soil microorganisms. The main soil-soluble salts are sodium, calcium, magnesium and potassium cations and chlorine anions. The salinity of the soil solution affects the osmotic potential and the structural stability of the soil [78]. Depending on electrical conductivity (EC), sodium adsorption ratio (SAR)

and pH, the soil is divided into three groups according to USDA (United States Department of Agriculture) classification:

- (1) saline soils – $\text{EC} > 4,0 \text{ dS m}^{-1}$, $\text{pH} < 8,5$, $\text{SAR} < 13$;
- (2) sodium soils – $\text{EC} > 4,0 \text{ dS m}^{-1}$, $\text{pH} < 8,5$, $\text{SAR} > 13$;
- (3) saline-sodium soils – $\text{EC} < 4,0 \text{ dS m}^{-1}$, $\text{pH} > 8,5$, $\text{SAR} > 13$.

The soil may be salted naturally and anthropologically. This applies to soils where the parent material is rich in soluble salts. Secondary salinity is the result of human activity. It is associated with poor irrigation and drainage of the soil, chemical contamination and incorrect fertilization [78]. High concentrations of salt ions (e.g. Na^+ , Cl^-) are harmful to plants, and salinity itself reduces the activity of microorganisms and changes their activity [2]. Osmotic stress caused by salinity causes cells to be dried out and lysed. Thus, the content of microbial biomass in the soil is also reduced [60]. Fungi are more susceptible to salt stress than bacteria, and therefore a higher bacterial-to-fungi ratio is observed in saline soils [74]. Some microorganisms have the ability to adapt or tolerate salinity in soil by synthesis and accumulation of osmolytes (e.g. proline, betaine, ectoine). Microorganisms called halophytes are particularly suited to high salt concentrations in the soil and produce enzymes resistant to salt and accumulate salt in their cells in quantities corresponding approximately to extracellular concentrations. Such microorganisms include *Halobacteriaceae* (archaea) and *Salinibacter ruber* (bacterium) [69]. Moreover, salinity was identified as the major factor of microbial community composition. Lozupone and Knight [44] research were based on an analysis of 21,752 RNA sequences isolated from 111 environmental samples from soils, sediments and water. Comparing the composition of the bacterial community in the analyzed samples, the researchers determined that salinity is the main determinant of microbiome composition and not the extremes of temperature and pH or other physical and chemical factors. Additionally, it was found that sediments are more phylogenetically differentiated than soil, which has high species-level diversity. Among the sequences obtained, many of them belonged to unnatural bacteria, and more than half of them were not related to literature reports. This indicates the importance of metagenomic studies in the context of environmental microbiology [44].

4. Soil temperature

Temperature is one of the most important edaphic factors determining the limits of microbial development because groups of microorganisms grow at the optimal temperature, and after exceeding this limit their growth is terminated [48]. Soil temperature affects

not only the activity of microorganisms but also seed sprouting, root growth and availability of nutrients. Soil temperature depends on the sunlight reaching the ground surface, water content, terrain topography, air temperature, soil properties and the vegetation [61]. Dry soils quickly warm-up, but also lose heat quickly. Moisture soils maintain their temperature longer, and heat is quickly transferred to the deeper layers. In the summer months, the deeper layers of soil are heated and cooled in the winter months. In 1961–1975, the average annual soil temperature in Poland was 8.9°C, at a depth of 5 cm and in the growing season 14.7°C [61]. As a result of the Ciaranek [7] research, it was found that in the years 2007–2009 in Krakow (Poland) the annual average soil temperature at the same depth was 11.7°C; to the depth of 20 cm it fell (to 11.1°C), and to the depth of 50 cm it again amounted to 11.7°C.

The microorganisms are divided into different groups depending on the temperature optimum: (1) psychrophiles which grow best in an environment below 10°C; (2) mesophiles which are the majority of soil bacteria and have the highest growth rate in the 20–45°C range; (3) thermophiles which grow at 50–65°C [52]. Psychrophilic soil microorganisms occur in the soils of eternal permafrost [77]. These include bacteria (e.g. *Halobacterium lacusprofundi*, *Sphingobacterium antarcticus*), fungi (e.g. *Penicillium jamesonlandense*) and archaeons (e.g. *Methanosarcina* sp.). Based on psychrotrophs, a microbiological consortium was developed: *Eupenicillium crustaceum*, *Paecilomyces* sp., *Bacillus* sp. and *B. atrophaeus* potentially used in agriculture to increase soil fertility [68]. In geothermally heated regions, e.g. volcanic soils, there are microorganisms called hyperthermophiles with an optimum growth rate of 80–113°C [31]. They belong to bacteria and archaea, the vast majority of which are archaea. Two species of *Picrophilus* bacteria have been isolated from dry, volcanic soils in Japan, which grow at 60°C while tolerating pH 0.7 [59].

Changes in soil temperature affect the diversity of the microbiome. The use of next generation sequencing (HiSeq, Illumina), has shown that an increase in soil temperature (up to 58°C) as a result of a continuous underground fire of coal mines located under the surface of the city Centralia (Pennsylvania, United States) caused a reduction in the diversity and number of microorganisms and a decrease in the number of antibiotic resistance genes in soil [11]. Researchers, also using 16S rRNA gene sequencing, found that the soils affected by the fire are highly dominated by a small number of taxonomic microbial units [40]. Temperature also influences the activity of enzymes secreted by microorganisms into the soil environment. It was shown that an increase in temperature stimulates the activity of nitrogenase, an enzyme produced by diazotrophs

bacteria that participates in the atmospheric nitrogen fixation [8]. Climate change, including an increase in temperature, also affects the structure and functioning of soil microorganisms [41]. Both, NGS (MiSeq, Illumina) and EcoPlate™ (Biolog Inc., Hayward, USA) methods were used in the research. Studies based on soil heating (mean soil temperature increase of 2.3°C) have shown that environmental warming has a significant impact on the metabolic potential of microorganisms. In heated soils, amines and carboxylic acids were rapidly decomposed [41]. In addition, it was demonstrated that soil heating has a significant effect on the soil fungal community and results in a decrease in the number of soil fungi to a greater extent than in the case of bacterial communities. Also with the use of classical analytical methods (soil respiration, soil biomass), it was shown that warming lasting longer than 3 years significantly affects the biomass of soil microorganisms [16]. Research using a combination of different research methods – both older and more recent (EcoPlate™, soil microbial biomass, PLFA) – has shown that microorganisms are able to adapt to a soil temperature increase of 1 to 2°C without disturbing the microbial structure [80].

An increase in temperature can also have the effect of dehumidifying the soil and reducing soil moisture, which is also an important edaphic factor affecting soil microorganisms.

5. Soil moisture

Soil moisture is defined as the water content of the soil. It is one of the most important physical parameters in agriculture, as it directly influences the growth of plants. A certain amount of water is stored in the soil. The water content of soil varies in time and space [78]. It depends on the soil properties, the type of vegetation, the intensity of evaporation (thus indirectly also on temperature), the amount and distribution of rainfall and irrigation in the case of arable land [54]. In Poland, precipitation is the primary source of water in soil [33].

Soil moisture affects the organisms living in the soil in many ways. Without the availability of water, microbial life is impossible. The water content of the soil affects the pH, the diffusion of solvents and gases and the availability of nutrients [75]. Water also enables the migration of microorganisms in the soil and the diffusion of compounds between the cells of organisms and the environment and is part of hydrolysis processes, and its content determines the rate of mineralization [34, 78].

Natural fluctuations in moisture associated with seasonal changes and precipitation are an important environmental factor in the metabolism of microorganisms. Recently, however, the frequency of floods and periodic flooding in Poland has been increasing and drought

Table I
Minimum value of water activity in the environment for various microorganisms

Water activity (a_w)	Microorganisms
1.00	<i>Caulobacter</i> , <i>Spirillum</i>
0.98	<i>Pseudomonas</i> , <i>Clostridium</i>
0.95	Gram-negative bacteria
0.91	<i>Bacillus</i> , <i>Lactobacillus</i>
0.88	<i>Saccharomyces</i> , <i>Candida</i>
0.85	Selected filamentous fungi (e.g. <i>Penicillium</i>)
0.80	Part of the yeast
0.75	Most of the filamentous fungi (e.g. <i>Aspergillus</i> , <i>Monascus</i>)
0.60	Halophytes (e.g. <i>Vibrio</i> , <i>Halomonas</i> , <i>Paracoccus</i>)

Based on Libudzisz *et al.* [43] and Kunicki-Goldfinger [37].

periods have been prolonged. Water stress caused by these phenomena affects soil microorganisms [79]. Some bacterial groups are very sensitive to alternating drainage and flooding conditions. These include, inter alia, autotrophic ammonia-oxidizing bacteria, which was confirmed by an analysis of 491bp segment of the *amoA* gene [19]. The researchers created the term water activity in the environment (a_w), which determines the ratio of the partial pressure of soil solution to the partial pressure of clean water and can be used to determine the water demand of microorganisms [37]. It is assumed that chemically pure water has $a_w = 1$.

Bacteria and archaea usually require more water activity to grow than fungi. Most bacteria require to grow $a_w > 0.91$, while most fungi and yeasts can grow at $a_w < 0.80$ (Tab. I).

The physical parameter – soil water potential (pF) [3] – is distinguished in the studies of the soil environment. The pF value of 0.00 corresponds to the full water capacity, which means that all soil pores are filled with water and pF = 4.2 is the point of permanent wilting of plants. In terms of soil water potential of soil microorganisms needed for development, microorganisms can be divided into three main groups:

Hygrophytes – developing at pF below 4.85 – bacteria, selected fungi;

Mesohygrophytes – developing at high pF but up to 5.48 – most fungi;

Xerophytes – capable of growth at a pF greater than 5.48 – some species from genera *Aspergillus* and *Monascus*.

The potential above which microbiological processes are no longer found is pF = 5.68 [3]. The highest values of microbiological activity in the soil are found at water potential of pF value between 2 and 4. The studies showed that the most optimal moisture content for

organotrophic bacteria is 20% of maximum water capacity (MPW), for *Azotobacter* and *Actinomyces* 40%, and for fungi 60% of MPW [5]. At 20% MPW the highest activity of enzymes such as dehydrogenases, catalase or acid and alkaline phosphatases was also observed.

Drought, *i.e.* a decrease in the water content of the soil, may result in an increase in the osmotic pressure of the soil and the formation of a hypertonic solution, which results in the drying out of microbial cells and reduces their activity and growth [56]. Lack of water also reduces the processes of carbon and nitrogen mineralization [78]. Drying the soil increases its oxygenation [34]. Some microorganisms are able to survive in such conditions in the state of anabiosis [43], *i.e.* in the state of extreme decrease in life activity. It is known that fungi are able to exist at lower a_w values than bacteria (Tab. I), for which the optimal a_w value is 0.98–0.99. The increase in bacteria was also observed at low water activity in the environment ($a_w = 0.75$), but it concerned halophilic bacteria of the genera *Halomonas*, *Paracoccus* and *Vibrio*. Halophilic microorganisms and those tolerating low water content have the same defence mechanism – they produce and accumulate osmolytes [78]. As the soil dries, access to nutrients is reduced. Restoring moisture in dry soil is linked to an increase in the number of microorganisms as a result of increased susceptibility to organic matter decomposition [75]. Moisture fluctuations occur naturally in soils in semi-dry and Mediterranean ecosystems, where the soil is often quickly wetted after long periods of drought [13]. Studies show that after 24 hours after irrigation of such dry soil, the maximum microbiological activity in the soil is observed [12]. However, with the increase in the number of drying and irrigation cycles, biomass and microbial activity in the soil decrease, nitrification is inhibited and fungal abundance is reduced, while the number of Gram-positive bacteria increases [78].

Excessive humidity caused by floods, melt or heavy rainfall also causes changes in the structure and activity of the soil microbiome. Increased humidity is associated with reduced oxygen and nitrogen diffusion in the soil [5] and the development of predators that feed on bacteria [34]. Under anaerobic conditions in the soil, the availability of micro and macro-elements is two to four times lower than in a well-oxygenated environment. In the structure of soil microbiome and its activity there are changes caused by soil flooding with water and oxygen loss [20]. Microorganisms start to use oxygen bound to *e.g.* NO_3^- and MnO_2^- , which leads to a reduction in these forms. Excessive irrigation and the associated lack of oxygen intensifies the development of anaerobic microorganisms, which in turn reduces the oxidative-reduction potential and intensifies the processes of reduction and fermentation [34]. Nitrate, manganese, sulphate and iron forms

are reduced [46]. Research using PLFAs indicate that with the loss of oxygen, the number of Gram-negative bacteria decreases and the number of Gram-positive bacteria in the soil increases [73]. Gram-negative fungi and bacteria normally occur in well-aerated soil layers. As a result of oxygen depletion, their number decreases [72, 73]. Among the anaerobic soil microorganisms are, among others, purple bacteria carrying out anaerobic photosynthesis – *Rhodospirillum* sp.; sulphate-reducing bacteria – *Desulfovibrio* sp., *Desulfotomaculum* sp.; and nitrogen-fixing bacteria – *Clostridium* sp.; as well as the representatives of archaea, who produce methane – *Methanobacterium* sp. [43]. As a result of the floods, a decrease in soil microbial biomass was observed and sulphate and nitrate-reducing bacteria were identified [72]. It was also found that the occurrence of intensive precipitation in vineyards increased the development of epiphytic microorganisms, including pathogenic fungi, e.g. *Botrytis cinerea* [63].

6. Organic carbon and nitrogen content

Soil organic matter is a basic indicator of soil quality, which determines its physicochemical properties and biological processes. High humus content in soils is, a factor stabilizing their structure, reducing susceptibility to compaction and degradation [49].

Carbon content plays an important role in the regulation of the diversity and structure of soil microbiome [82]. A research of 29 soil samples from four geographically distinct locations using a small-subunit (SSU) rRNA-based cloning approach demonstrated that carbon-poor soils had microbial composition shifts associated with soil depth [82]. It was shown, that deeper soil communities were less diverse and had strongly dominant genera, whereas surface communities had more an operational taxonomic unit (OTU). It was demonstrated, based on quantitative PCR (qPCR) of genes encoding the key enzymes of ammonia oxidation (*amoA*), nitrate reduction (*narG*) and denitrification (*nirK*, *nirS*, *nosZ*), that the forms of soil carbon (*i.e.* inorganic, organic) affects the structure of denitrification communities, but does not regulate their numbers [29]. Among the microorganisms preferring carbon-rich environments (*e.g.* rhizosphere) based on bacterial and archaeal 16S rRNA sequenced, one can distinguish *Alphaproteobacteria* [28].

Nitrogen in soil is a mobile component that undergoes a number of environmental changes: ammonification, nitrification, denitrification or sorption. Many of these processes involve bacteria, so it is understandable that the amount of nitrogen in the soil determines the number of bacterial communities in the soil [70]. The source of nitrogen in the soil is both mineral and

organic fertilization, decomposition of plant residues, as well as free nitrogen binding by symbiotic bacteria *Rhizobium* or free-living assimilators – *Azotobacter*, *Arthrobacter*, *Beijerinckia*, and *Clostridium*.

The type of nitrogen fertilizer used (*e.g.* urea, sewage sludge, ammonium sulphate, calcium nitrate, manure) has a significant effect on soil pH [27]. Fertilization with *e.g.* ammonium nitrate causes pH decrease in soil by as much as 1.4 and consequently affects the communities of soil bacteria, which was confirmed by pyrosequenced analysis [58]. The use of organic fertilizers increases the number of endophytic nitrifiers in soil [55].

7. Heavy metals content

Heavy metals are naturally present in each soil at a non-hazardous level. However, exceeding certain standards is very harmful. Excessive concentrations of heavy metals in the soil are due to human activity, including, but not limited to, crop errors. Among heavy metals, there are harmful elements such as cadmium, lead, mercury, nickel and arsenic, but also high concentrations of zinc and manganese [1].

Using pyrosequencing, it was shown that in Polish soils zinc decreased both bacterial diversity and species richness. In soils contaminated by zinc, lead and chromium it was possible to delineate the core microbiome, which comprised members of such taxa as *Sphingomonas*, *Candidatus Solibacter* and *Flexibacter* [22]. Using the high-throughput Illumina sequencing of 16S rRNA gene amplicons it was determined also, that bacteria have different reactions to heavy metals. The bacteria that positively correlated with Cd were, among others, *Acidobacteria* Gp and *Proteobacteria*. A negative correlation was found in *e.g.* *Longilinea*. Analysis the effects of heavy metals on a soil microbial community using DGGE showed that exposing soil to heavy metals changed the microbial community structure representing dominant but also minor populations [25]. Based on the number and type of OTU obtained, the researchers found that the soil bacteria community can adapt to long-term heavy metal contamination through the change in microbial community composition and structure, rather than the change in their species diversity and evenness [42]. The metal-resistant bacteria include the genus *Thiobacillus*, which showed a significant positive correlation with cadmium, zinc, arsenic, and lead indicating that the genus was tolerant to heavy metal [42]. The study conducted on the paddy soils along a nonferrous smelter in South Korea showed, that the phylum *Proteobacteria* was found to predominate in all samples, regardless of the heavy metal concentration. Used the 16S rRNA gene pyrosequencing authors found, that only in the case of the

phylum *Chlorobi*, a strong negative impact of the soil cadmium concentration was revealed [71]. Researchers concluded that the diversity in the bacterial community structure at the phylum level was mostly related to the general soil properties, while at the finer taxonomic levels, the concentrations of arsenic and lead were the significant factors affecting the community structure [71]. Analyses of the bacterial community response to arsenic and chromium contamination revealed by pyrosequencing researchers showed that in non-contaminated soils the dominant phylum was *Actinobacteria*, whereas in contaminated soils it was *Proteobacteria*. In addition, in contaminated soils a decrease in OTUs number of 14–38% was observed in comparison to control soils. The decrease in bacterial diversity within the contaminated soils was confirmed by species richness (Chao, ACE, Shannon) based on pyrosequencing data [67]. The qPCR and PCR-DGGE analysis on samples from agricultural soils near manufacturing district suggests that heavy metal pollution has significantly decreased abundance of bacteria and fungi and also changed their community structure [10]. Researchers analysed the contaminated landfill soils of Peninsular Malaysia showed, that *P. mendocina* has the highest resistance to metal exposure. When *B. pumilus* was absolutely resistant to the heavy metals used in the study, except nickel [32]. Examination of lead-contaminated soils by high throughput amplicon sequencing showed that *Verrucomicrobia* were less abundant at high contamination level whereas *Chlamydiae* and γ -*Proteobacteria* were more abundant [64].

Unlike bacteria, in the research provided by Li *et al.* [42] the members of the archaeal domain, *i.e.* phyla *Crenarchaeota* and *Euryarchaeota*, class *Thermoprotei* and order *Thermoplasmatales* showed an only positive correlation with Cd. The researchers stated that archaea were resistant to heavy metal contamination and can contribute to its adaptation to heavy metal. Also in other environment contaminated with heavy metals (anoxic freshwater lake sediments) was found that *Crenarchaeota* was associated with metal contamination [24].

The presented researches indicate that the heavy metal content affects the distribution of microbial population in the soil. Some types are resistant or even prefer environments with high metal content, but most data indicate a decrease in the number and variety of microorganisms, especially bacteria, in soil with increased contamination.

8. Conclusion

The most important abiotic factors influencing soil microorganisms are described in this review. Apart from the edaphic factors described above, the soil nutri-

ent content in available forms, toxic compounds, light and oxygenation can be distinguished. There are complex relationships between these factors since salinity affects the pH of the environment, temperature affects the water content of the soil, and both the presence of salt and humidity depending on the type of structure of the soil. The different taxonomic units of microorganisms are characterized by different ecological optimum. This is important from the point of view of agriculture, because human intervention in the soil environment may cause changes which will have a negative or positive impact on microorganisms. Microorganisms are known for their many adaptation mechanisms, but they still have environmental tolerance limits, beyond which they lose their viability or die. Maintaining constant conditions optimal for a given soil environment provides for the development and activity of the microbial community.

The use of new research methods in environmental microbiology allows for a more detailed examination of soil microbial contamination, but the vastness of the links between the various components of the soil environment is so great that much remains unknown.

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