

Actinomycetes as an indicator of the quality and health of agricultural soil

Aktinomycéty ako ukazovateľ kvality a zdravia poľnohospodárskej pôdy

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ABSTRACT

Soil quality and health can be assessed in both natural and agricultural ecosystems using indicators that sensitively reflect, in particular, adverse disturbances in these complex environments. However, selecting appropriate indicators is complicated by the complexity of soil, its previous use, and climatic influences. In addition to physical and chemical parameters, assessments often include organic matter, xenobiotics, and biological indicators. Among biological indicators, it is recommended to monitor microorganisms – not only their abundance, but also their activity. In addition to genetic, functional or biochemical diversity, microbial biomass, respiration and enzyme reactions, selected microbial groups also respond to changes in the soil environment. It is most often recommended to evaluate oligotrophic and nitrogen-fixing bacteria, microscopic filamentous fungi, and, in recent years, actinomycetes. This article summarises current knowledge confirming the importance of evaluating actinomycetes as sensitive indicators of soil quality and health. Their indicator value is mainly related to their significant contribution to the decomposition of organic matter, suppression of pathogens, improvement of soil structure and rapid response to changes in pH and conductivity. Their ability to fix nitrogen and biocontrol activity are also important for increasing fertility. Soils with high activity of non-pathogenic actinomycetes are characterised by healthy, fertile and biologically stable soil.

Keywords: attribute, plant nutrition, soil, streptomycetes, sustainability

ABSTRAKT

Kvalitu a zdravie pôdy možno hodnotiť v prírodných aj poľnohospodárskych ekosystémoch pomocou indikátorov, ktoré citlivo odrážajú najmä negatívne zásahy do tohto komplexného prostredia. Výber vhodných ukazovateľov však komplikuje zložitosť pôdy, jej predchádzajúce využívanie a klimatické vplyvy. Popri fyzikálnych a chemických parametroch sa často hodnotia organická hmota, prítomnosť xenobiotík a biologické indikátory. Z biologických ukazovateľov sa odporúča sledovať mikroorganizmy, a to nielen ich početnosť, ale aj ich aktivitu. Okrem genetickej, funkčnej či biochemickej diverzity, mikrobiálnej biomasy, respirácie a enzýmových reakcií reagujú na zmeny v pôdnom prostredí aj vybrané mikrobiálne skupiny. Najčastejšie sa odporúča hodnotiť oligotrofné a nitrogénne baktérie či mikroskopické vláknité huby a v posledných rokoch aj aktinomycéty. V článku sumarizujeme aktuálne poznatky, ktoré potvrdzujú význam hodnotenia aktinomycét ako citlivého indikátora kvality a zdravia pôdy. Indikátorová hodnota aktinomycét súvisí najmä s ich významným podielom na rozklade organickej hmoty, potláčaní patogénov, zlepšovaní pôdnej štruktúry a rýchlej reakcii na zmeny pH a vodivosti. Pre zvyšovanie úrodnosti sú dôležité aj ich schopnosť fixovať dusík a biokontrolná aktivita. Pôdy s vysokou aktivitou nepatogénnych aktinomycét sú kvalitné a zdravé, úrodné a biologicky stabilné.

Klíčovú slová: atribút, pôda, streptomycéty, udržateľnosť, výživa rastlín

INTRODUCTION

According to Bhaduri et al. (2022), soil is a heterogeneous, living, and dynamic system that is crucial for maintaining an entire ecosystem. Acton, Gregorich (1995) describe that soil can absorb organic material, from which it can recycle nutrients and provide them to plants for their growth, and can also retain and reduce some forms of toxic substances. It can act as a natural filter, purifying water and air and providing an environment for the exchange of atmospheric gases, thus directly affecting the global climate. The attribute of soil quality and health is often defined differently in the professional literature. Soil assessment can be carried out from several points of view and with different intentions, depending in particular on the purposes for which the land is and will be used. In the case of agriculturally used soils, attributes such as productivity, resilience, and soil degradation, but also the attributes of soil quality and health, are evaluated (Bünemann et al., 2018). Soil quality is one of the three components of environmental quality, in addition to water and air (Andrews et al., 2004). This assessment focuses on the ability of soil to support plant growth, but is commonly defined much more broadly as "the ability of soil to function within ecosystem and land-use boundaries to maintain biological productivity, environmental quality, and promote plant and animal health" (Doran and Parkin, 1994; Doran and Parkin, 1996). Factors such as mother material, climate, topography and hydrology can affect potential values of soil properties to such an extent that it is not possible to set universal targets, at least not in absolute numbers. Therefore, the assessment of soil quality must include baselines or benchmarks in order to identify management impacts. Soils are often slow to respond to changes in land use and management, and therefore, it can be more difficult to detect changes in soil quality before irreversible damage occurs than in the case of water and air quality (Nortcliff, 2002).

The presented review aimed to complete all currently available information published in scientific peer-reviewed journals, which confirms that actinomycetes are a suitable and sensitive indicator of soil quality and health attributes and are an important part of soil microbiocenosis.

SOIL QUALITY AND HEALTH, AND ITS EVALUATION

In current scientific publications, it is often observed that authors mainly refer to works from the late 20th century, which were groundbreaking in this field and are still used today in their original or modified form. Sarkar et al. (2022) cite the work of Acton and Gregorich (1995), who state that in the past, the attribute of soil health was evaluated in the agricultural sector only by the quantity and quality of plant biomass produced. At the end of the 20th century, according to them, this idea was gradually abandoned, and soil began to be perceived as part of an ecosystem in which it interacts with all its components. Along with this change, it was necessary to reconsider the very definition of the soil health attribute. According to Sarkar et al. (2022), this attribute is "the ability of the soil to promote plant growth without causing degradation or other environmental damage". They further state that healthy and high-quality soil must provide suitable conditions for the growth of plants and microorganisms, can regulate water and also perform the function of a "natural buffer". They also recommend monitoring other parameters such as pH, organic matter content, soil structure and soil susceptibility to erosion. According to the SSSA (Soil Science Society of America) commission, each term should have its own definition (Karlen et al., 1997). Amat et al. (2020) and most authors refer to the definitions of soil quality and health defined by Doran et al. (1996) and Karlen et al. (1997). According to Doran et al. (1996), it is "the ability of the soil to function as a living vital system within the boundaries of an ecosystem to maintain biological productivity, maintain air and water quality, as well as the health of plants, animals, and humans." Karlen et al. (1997) present the so-called simplified version of the definition of the soil quality attribute, which they state as "the ability of the soil to perform its functions under given physical, chemical and biological properties. From the physical indicators, they recommend monitoring the evaluation of soil structure, porosity, aggregate stability, saturated hydraulic conductivity, salinity, infiltration, soil bulk density, topsoil depth, or soil retention capacity. Biological indicators include the mineralisation of nitrogen, plant root pathogens, soil bio-

diversity, the structure of the soil food chain, and plant biodiversity. According to these authors, soil quality and soil health are two different attributes, with mineral composition, soil texture and topsoil depth not being significant for assessing soil health, and indicators such as soil biodiversity, soil food chain structure and plant biodiversity not being important for assessing soil quality.

Obi et al. (2024) summarised the basic indicators of soil quality into six groups, namely soil texture, soil compaction, soil fertility, organic matter, soil structure, soil biological activity and soil response. They recommend monitoring the basic properties of soil solids, soil solutions, soil atmosphere, plants and other soil organisms. They describe that when evaluating the soil quality attribute in practice, it is first necessary to identify problems with land use, followed by the selection and interpretation of appropriate indicators. However, it must be taken into account that these activities are influenced by the basic characteristics of the soil (such as texture, organic matter content, pH, cation exchange capacity – CEC, porosity, etc.), as well as by environmental conditions (climate, topographical, hydrological and biological factors) and anthropogenic influences, in particular land use and management.

In their review study, Bhaduri et al. (2022) state that current methods of assessing the state of soil health cannot provide a complete picture of the given state of a functional soil system, as they lack an indication of the dynamic changes in how the soil responds to stress caused by anthropogenic activity or other disturbances of its internal environment. They recommend a comprehensive determination of the characteristics of the soil microbial community and the biogeochemical properties that affect the soil. From the biological indicators (bioindicators), they propose to evaluate 4 parameters, namely physiological (carbon, phosphorus and nitrogen of microbial biomass, and substrate-induced respiration), metabolic (enzymatic activity), functional (assessment of the presence of a specific microbial community) and genetic (extraction of soil environmental DNA and RNA

in evaluation of total biodiversity). They state that more effective biological indicators of the state of soil health at the ecosystem level need to be determined for the future. According to these authors, microbial indicators that provide information about the biomass, activity, or functionality and diversity of microbial communities are a reflection of soil health. In most publications, the authors agree with the indicators proposed by Doran and Jones (1996) and are presented in Table 1. According to their distribution, the physical and chemical indicators are basically identical to the above-mentioned works. Biological indicators and the presence of xenobiotics, such as the persistence of pesticides, are different. Biological indicators were described by Bhaduri et al. (2022) as very variable and dynamic, as they respond quickly to changes in the soil environment. Among such indicators, Doran and Jones (1996) included, in comparison with the above-mentioned authors, e.g. the decomposition of cellulose. This, along with microbial respiration, is the most commonly used indicator (Sarkar et al., 2022). Its resulting values are important in terms of monitoring and evaluating the carbon cycle in the soil, which is also directly related to ongoing climate change (Ananyeva et al., 2020). The most commonly used indicators are the presence and size of microbial biomass, the ability to mineralise nitrogen, the growth rate, structure and overall diversity of the microbial community. The values of this indicator are crucial for soil health, as it is the soil microcosm that is responsible for the implementation of many important soil functions (Sarkar et al., 2022). Another of the recommended indicators is directly related to microbial biomass, which is the evaluation of enzyme activity, especially dehydrogenases. This is a reflection of the activity of chemoheterotrophic bacteria, actinomycetes, and microscopic fungi. Among enzymes, those that confirm hydrolytic activity and influence the course of carbon, phosphorus, nitrogen and sulfur cycles in the soil are also evaluated. This indicator is recommended by several authors, such as Ghosh et al. (2020), Tomar and Baishya (2020), Amat et al. (2020), and Chettri et al. (2021).

Table 1. Summarisation of the proposed indicators for the assessment of the soil quality and health attribute

| Indicator | Authors | Indicator | Authors |
|-----------------------------------|--------------------|---|--------------------|
| Physical Indicators | | | |
| Soil fertility | 1); 5) | Soil structure (texture) | 1); 2); 3); 4); 5) |
| Soil susceptibility to erosion | 1) | Characteristics of the soil profile | 2) |
| Depth of over-rooting | 2); 4); 5) | Overall morphological characteristics of the soil | 2) |
| Soil salinity | 3) | Bulk weight of soil | 2); 3); 4); 5) |
| Soil porosity | 2); 3); 4) | Stability of soil aggregates | 2) |
| Soil compaction | 2); 5) | Soil moisture | 2) |
| Water infiltration | 2); 3); 5) | Conductivity | 2); 3); 4); 5) |
| Hydrolimits | 2) | Topsoil depth | 3) |
| Particle bonds in soil | 3) | Soil retention capacity | 3); 4) |
| Soil color | 5) | Soil temperature | 5) |
| Mineral composition of the soil | 4) | | |
| Chemical Indicators | | | |
| Soil reaction | 1); 2); 3); 4); 5) | Conductivity of the solution | 2) |
| Mineral n content | 2); 3); 4); 5) | P and K content in the soil | 2); 4); 5) |
| Soil exchange capacity | 3); 4); 5) | Total soil fertility | 3); 5) |
| Adsorption capacity of the soil | 3) | Amount of carbon In the soil | 3) |
| Soil organic matter | 4); 5) | Heavy metals in soil | 4) |
| Biological indicators | | | |
| Soil respiration | 2); 3); 4); 5) | Cellulose decomposition | 2) |
| Microbial biomass | 2); 3); 4) | Mineralizable n | 2); 4) |
| Growth rate | 2) | Activity enzymov | 2); 3); 4); 5) |
| Microbial community | 2); 4); 5) | Soil invertebrates | 2); 3); 5) |
| Infection of roots with pathogens | 2); 4) | Mycorrhizal relationships | 3) |
| Abundance of microorganisms | 4) | Structure of the soil food chain | 4) |
| Plant growth | 4) | Plant biodiversity | 4) |
| Organic matter | | Xenobiotics | |
| Organic C, N | 2); 5) | Polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), pesticide residues | 2) |

¹⁾ Acton and Gregorich (1995);²⁾ Doran and Jones (1996);³⁾ Karlen et al. (1997);⁴⁾ Pankhurst et al. (1997);⁵⁾ Obi et al. (2024).

ACTINOMYCETES AND THEIR CHARACTERISTICS

Doran, Jones (1996), Bhatti et al. (2017), and Bhaduri et al. (2022) recommend monitoring oligotrophic and nitrogenous bacteria, microscopic fungi and actinomycetes from bioindicators of soil quality and health.

According to Yaradoddi et al. (2022), actinomycetes are a broadly expansive group of Gram-positive, aerobic, spore-forming filamentous bacteria. Bouizgarne (2022) states that actinomycetes are prokaryotic microorganisms, mostly obligate aerobes. Their designation "filamentous bacteria" is related to the common morphological features with filamentous microscopic fungi. Actinomycetes, from a cytological point of view, are prokaryotic organisms that have some differences in the composition of the cell wall. Barka et al. (2016) and Javed et al. (2021) state that the chemical structure of peptidoglycan in the cell wall of actinomycetes is the key information based on which actinomycetes can be taxonomically differentiated down to the genus level. Within the chemical structure of peptidoglycan, it is important to determine the presence of an amino acid at position 3 in the tetrapeptide side chain, the presence or absence of the amino acid glycine in interpeptide bridges, or the sugar content of peptidoglycan. They also identify the presence or absence of optical isomers of the chiral non-proteinogenic amino acid 2,6-diaminopimelic acid (DAP) as important. This can be found in the cell wall of actinomycetes, either in the form of an LL- or DL- isomer. In their work, Barka et al. (2016) describe differences in the composition of cell walls even in specific genera. For example, the species of the genus *Streptomyces* contains both LL-DAP and glycine in its cell wall. The cell wall of the species of the genus *Actinomyces* and *Micromonospora* also contains glycine, but contains the DL-isomer DAP and among the sugars, it contains arabinose and xylose. Other species of genera of actinomycetes, such as the genus *Frankia*, *Microbispora* or *Thermoactinomyces*, do not contain glycine in their cell wall, and the genus *Actinomyces* does not contain DAP. There are also differences between individual genus representatives in the presence of individual amino acids, fatty acids, phospholipids

or isoprenoid quinones. For this reason, when evaluating the phenotypic diversity of actinomycetes, the authors recommend combining the analysis of the DAP profile with other phenotypic or genotypic criteria. This is mainly due to the high proportion of guanine and cytosine in deoxyribonucleic acid. Yaradoddi et al. (2022) report this value in the range of 57-75%, and Gupta et al. (2020) report a range of 66-72% for the genus *Frankia*, Gao et al. (2022) for the strain *Streptomyces paradoxus* D2-8, an exact value of 71.15% and Zhuang et al. (2021) for the genus *Nocardia* sp., a value of 67.8%. In addition to a high percentage of G+C (> 70%), species of the genus *Streptomyces* also have linear, medium-sized genomes (8-10 Mb), which are considered special features among bacteria (Hopwood, 2019). According to this author, they are bacteria with many original features, e.g. their genome is linear (not circular) with a unique way of replication, as they transfer their chromosome from donor to recipient by a conjugation mechanism, but this is radically different from the paradigm of *Escherichia coli*. They have twice as many genes as a typical rod-shaped bacterium (*Escherichia coli* or *Bacillus subtilis*), and the genome typically carries 20 or more gene clusters encoding the biosynthesis of antibiotics and other specific metabolites, of which only a small fraction is expressed under typical laboratory screening conditions. This means that there are a huge number of potentially significant compounds that can be discovered when these "dormant" genes are activated. These natural products with high structural diversity belong to the group of macrolides, tetracyclines, aminoglycosides, glycopeptides, ansamycins and terpenes. For example, *Streptomyces hygroscopicus* secretes approximately 180 metabolites with a wide range of bioactivities (Alam et al., 2022).

The morphological difference of actinomycetes from prokaryotes and similarity to microscopic filamentous fungi is most characterised by the formation of substrate and air, so-called mycelium, formed from a single cell (Katti et al., 2022). Das et al. (2021) and Al-Quwaie (2024), in turn, report that this mycelium has its characteristic powdery structure on nutrient soils and is char-

acterised by a radial arrangement with multicoloured pigmentation and a typical earthy smell, which is caused by the production of geosmin (Devi et al., Kiran et al., and Rekadwad et al., 2022). The substrate mycelium is typically monopodial, branched, which means that the main hyphae maintain a dominant position and grow straight, with lateral branches growing from it. For example, representatives of the genus *Thermoactinomyces* have a different way of branching (dichotomous), in which the fibre is divided into two approximately equal parts, neither of which is dominant. In addition to the highly differentiated and permanent mycelium, typical of representatives of the genera *Streptomyces* or *Frankia*, this mycelium can break into fragments (*Nocardia*) (Katti, 2022). In their work, Barka et al. (2016) describe that the main function of the substrate mycelium is to draw nutrients necessary for the growth of actinomycetes, and therefore it grows into the nutrient medium, possibly inhabiting its surface. This mycelium is usually thin and more branched than the aerial mycelium, which grows from the substrate mycelium and whose formation depends mainly on the surrounding environmental conditions. Van Bergeijk et al. (2020) and Pacios-Michelena et al. (2021) specify that the production of aerial mycelium by actinomycetes is controlled by genes labelled *bld* (*bald*) and *whi* (*white*). The fibrous growth of hyphae and complex specialised metabolism evolved to facilitate interactions with plant roots, presumably to allow entry into root tissue and allow them to compete for food in the form of root exudates or more complex polymers that make up the cell wall of the plant. Actinomycetes reproduce only asexually and not by transverse division like most bacteria, but by the formation of spores. These can be formed singly or in chains, from substrate (*Micromonospora*, *Micropolyspora*, *Thermoactinomyces*) and aerial mycelium (*Streptomyces*). According to Li et al. (2016), they can also arise in specialised formations called sporangia and can be mobile thanks to flagella (*Actinoplanes*, *Pilimelia*). With enough nutrients, humidity and temperature, these spores are formed by the germination process of fibres/hyphae. Through spores, actinomycetes can survive various adverse conditions. As an example, the spores of

representatives of the genus *Streptomyces*, which are resistant to UV radiation, nutrient deficiencies and dehydration, allow them to survive in various environmental conditions (Hungund et al., 2022).

Das et al. (2021) report that although actinomycetes have some bacterial characteristics and some fungal properties, their growth is slower compared to other soil microorganisms. Therefore, in a heterogeneous biological complex such as soil, with the constantly ongoing competition of microorganisms for accessible sources of energy and building materials, they must use mechanisms that allow them to compensate for this disadvantage. Such basic mechanisms include the production of secondary metabolites in the form of substances such as antibiotics, hydrolytic enzymes, volatile organic compounds (VOCs) or siderophores (Yan et al., 2021). The ability of actinomycetes to produce various specific metabolites reflects their overall adaptability, necessary to survive in such a competitive environment (Dow et al., 2023). These biomolecules are usually synthesised by polyketide synthase (PKS) and non-ribosomal peptide synthase (NRPS), whereby the genes responsible for this synthesis are grouped into so-called clusters. However, the activity of many clusters may still be subdued, but their activation may lead to the discovery of other important bioactive metabolites in the future (Ngamcharungchit et al., 2023).

OCURRENCE OF ACTINOMYCETES IN SOIL

The species of the genus *Streptomyces* are widely distributed in soils in a variety of environments, including forests, prairies, deserts, tundra, and agriculturally exploited lands. Their spores are spread by wind and water (Subramani and Aalbersberg, 2012). Worldwide, the population density and diversity of *Streptomyces* are influenced by soil characteristics such as pH, moisture and nutrient content. Soils with lower pH values and nutrient deficiencies tend to have a lower diversity of *Streptomyces* (Hirsch and Valdés, 2010). Unique strains of the genus *Streptomyces* are often isolated from extreme environments such as volcanic ash, deep-sea sediments, cold deserts, and hyperarid soils (Sivalingam et al., 2019).

Bouizgarne (2022) and Hungund et al. (2022) state that the presence of actinomycetes in the soil profile depends on environmental conditions and basic physicochemical properties of the soil. It is estimated that 10^4 to 10^9 CFU of actinomycetes are present in 1 g of soil, especially in soils with a high concentration of organic matter (Barka et al., 2016; Bhatti et al., 2017; Harir et al., 2018). Hamid et al. (2020) report that actinomycetes, belonging to the genus *Streptomyces*, are also undemanding in terms of humidity and are present in arid regions. This corresponds to the claim of Yaradoddi et al. (2022), who state that actinomycetes are ubiquitous and populate both dry soils and soils with higher pH values. According to Tarafdar (2022), most actinomycete species have the highest occurrence in soils with a soil reaction with neutral soil pH values. In terms of temperature, the range in which these microorganisms can survive is really wide. Most species are mesophiles with an optimum of 25-30 °C; however, some psychrophilic species also occur in environments with a temperature of only around 5 °C, and thermophilic actinomycetes inhabit environments with temperatures up to 80 °C (Yaradoddi et al., 2022). According to Das et al. (2021), the temperature range of thermophilic species of the genera *Thermoactinomyces* and *Streptomyces* is 55-65 °C. As an example of thermophilic actinomycetes, they cite species of the genera *Thermoactinomyces* and *Streptomyces*, which are present at higher temperatures in composts or in manure, showing a higher sensitivity to lower pH values and excessively humid conditions.

According to Mishra et al. (2022), actinomycetes are able to survive even in extreme conditions, such as saline soils, and are also an important part for plants in overcoming this abiotic stress. Nazari et al. (2022) report that some halotolerant actinomycete species survive even in environments with 32% NaCl content. Rao and Li (2022) describe that one of the mechanisms of adaptation of actinomycetes to a saline soil environment is the production of cyclic amino acids such as glycine, serine, and threonine. The ability of actinomycetes to grow and positively affect plant growth under such conditions was confirmed by Meena et al. (2020) and Zhu et al. (2024)

in wheat cultivation, Nozari et al. (2022) in maize cultivation, Niu et al. (2022) in rice cultivation, and Gao et al. (2022) in evaluating the effect of actinomycetes on soybean resistance to saline soil conditions.

Actinomycetes are mainly found in the soil in the upper layers, which are best aerated and have a high content of available nutrient sources (Ngamcharungchit et al., 2023). According to Edison and Pradeep (2020), Das et al. (2021), Javed et al. (2021), and Ravi (2022), actinomycetes are often present in the rhizosphere region, where they can act as colonisers of the root system. Their presence in the root zone area has a significant positive effect on plant health (Kontro, Yaradoddi, 2022). For this reason, in their publication, Dow et al. (2023) hypothesise that the appearance of actinomycetes in the rhizome area is controlled by the plants themselves, as they are beneficial to the plant. In addition to helping plants overcome various forms of biotic and abiotic stress near the roots, they improve nutrient uptake through the use of molecular nitrogen fixation, solubilization, and chelation. Kontro et al. (2022) report that these prokaryotic microorganisms can also completely suppress pathogenic microscopic filamentous fungi and bacteria in the rhizosphere, or can minimise their harmful effects. Javed et al. (2021) report that by such antagonistic activity towards root phytopathogens, they maintain the so-called biotic balance in the rhizosphere. Edison and Pradeep (2020), as well as Ravi (2022), report that with the depth of the soil profile, the number of actinomycetes gradually decreases. However, Barka et al. (2016) and Bouizgarne (2022) state in their publications that species of the genus *Streptomyces* sp. are also found at a soil profile depth of more than 2 meters. In terms of trophic, actinomycetes are saprotrophic, obtaining the necessary carbon and energy from the decomposition of mainly dead organic matter, of plant, animal and microbial origin (Bouizgarne, 2022). They are also adapted to the decomposition of complex polysaccharides, thus contributing to the decomposition of even more difficult to decompose organic substrates and to the formation of soil humus (Javed et al., 2021). In addition to being saprotrophic, actinomycetes are also endophytic, as they also inhabit the inter-

nal tissues of plants, namely roots, stems, leaves, flowers, fruits, or seeds (Sooriyaarachchi et al., 2021). Rao and Li (2022) and Dow et al. (2023) report that actinomycetes are most abundant in the endosphere of roots, compared to the rhizosphere, loose soil or the aerial part of plants. Endophytic actinomycetes are metabolically more active than those that live in loose soil. This is a consequence of their specific activity inside plant tissues, in which they activate other metabolic pathways (Kumar et al., 2020). More different metabolites produced help them to mediate better communication with the host and the microbiome present (Dow et al., 2023). Frequently occurring endophytic actinomycetes include representatives of the genera *Streptomyces*, *Frankia*, *Micromonospora*, *Microbispora*, *Streptosporangium*, *Nocardioides*, and *Nocardia* (Katti et al., 2022).

CULTIVABLE ACTINOMYCETES AND THEIR SOIL ACTIVITIES

Actinomycetes, cultivable in laboratory conditions, are most often classified in the genus *Streptomyces*; they are commonly referred to as streptomycetes. Edison and Pradeep (2020) and Nazari et al. (2022) list more than 500 described species of streptomycetes, Pacios-Michelena et al. (2021) list more than 700 species, but Aryal et al. (2021) list more than 850 described species of streptomycetes. According to Das et al. (2021), this is less than 70% of the total predicted population of cultivable soil actinomycetes. However, Bouizgarne (2022) as well as Silva et al. (2022) report a value of up to 95%, Sapkota et al. (2020) evaluated the percentage ratio of representatives of the genus *Streptomyces* at 70.7% from eleven soil samples.

They are specific, as stated by Yaradoddi (2022), by the extensive production of secondary metabolites, which include antibiotics, antivirals, antihypertensives, anticancer agents, fungicidal agents or immunosuppressants. Studies indicate that this genus is capable of forming 150,000 bioactive compounds (Lacey and Rutledge, 2022). Hungund et al. (2022) report that streptomycetes (*Streptomyces griseus*, *S. kanamyceticus*, *S. fradiae*, *S. hygroscopicus*, *S. pristinaespiralis*, *S. mediterranei*) are the

most important producers of substances such as streptomycin, kanamycin, neomycin, hygromycin, pristinamycin, and rifamycin. In addition to medicine, these substances are often used in agriculture, especially in the fight against phytopathogens. For example, the effectiveness of casugamycin, streptomycin and oxytetracycline against the phytopathogenic bacterium *Erwinia amylovora*, which causes bacteriosis of fruits, has been confirmed (Slack et al., 2021). According to Aallam et al. (2022), metabolites of representatives of the genus *Streptomyces* are part of more than 70% of products used in medicine and agriculture. This high production of bioactive metabolites is also genetically determined, as streptomycetes have multiple biosynthetic gene clusters (BGCs) on each genome, which are the source of many bioactive compounds with medicinal or agricultural use (Nicault et al., 2021). It is very often reported to be antifungal and effective against phytopathogens of the genus *Fusarium* (Aallam et al., 2022; El Sharkawy et al., 2022; Nazari et al., 2023; Djemouai et al., 2023; Kawicha et al., 2023). Other authors (Elshafie and Camele, 2022; Nazari et al., 2023; Zhu et al., 2023) also report antifungal activity against phytopathogenic representatives of the genera *Pythium*, *Rhizoctonia* and *Sclerotinia* in their works. Jia et al. (2023), in turn, confirmed the efficacy of *Streptomyces tauricus* XF against yellow wheat rust (*Puccinia striiformis* f. sp. *tritici*) (Table 2). However, the efficacy of these bioactive metabolites against specific phytopathogens varies across species (Nazari et al., 2023).

ACTINOMYCETES AS AN INDICATOR OF SOIL QUALITY AND HEALTH ASSESSMENT

According to Hermans et al. (2020) and Hamaila et al. (2024), soil microorganisms are an important bio-indicator of soil quality and health and play an important role in predicting and promoting crop development. The term bioindicator in connection with microorganisms is defined in their publication by Neemisha and Sharma (2022) as microorganisms (or a group of microorganisms), their part or product, a biological process by which information can be obtained about the quality of the entire environment, or part of it. According to Bhaduri et al. (2022), a bioindicator is a species or group of species of

microorganisms that reflects biotic and/or abiotic levels of environmental pollution.

Several authors such as Bhatti et al. (2017), Javed et al. (2021), Nazari et al. (2022) and Hungund et al. (2022) cite actinomycetes, as organisms that should be used as an indicator of the soil health attribute, as they affect many of its important processes and other indicators and parameters such as pH, electrical conductivity, bioadsorption of heavy metals, or enzymatic activity (Ali et al., 2021a) and, according to Nazari et al. (2022), soil fertility and fixation of atmospheric nitrogen and their biocontrol activity.

According to Javed et al. (2021), actinomycetes belong to a group referred to as PGPB (plant growth-promoting bacteria) or, as stated in their paper, Bhatti et al. (2017) and Dasila et al. (2020), belong to the category

labelled PGPR (plant growth-promoting rhizobacteria). They state that they can influence plant growth through direct and indirect mechanisms. Indirect mechanisms include mainly the ability of actinomycetes to suppress the growth and occurrence of pathogens, either in the form of colonisation or antagonism through the biosynthesis of antibiotics and other secondary metabolites. Bouizgarne (2022) also complements these indirect mechanisms by stimulating the induced defences of plants. This ability has been demonstrated in their works, for example, by Tran et al. (2021), El Sharkawy et al. (2022) and Jia et al. (2023), who report that the presence of streptomycetes increased the expression of the JERF3 gene, pathogenesis-related proteins (PR1, PR2, PR3, PR4, PR9, PR10) in the plant and induced the expression of pathways, associated with the production of salicylic acid and jasmonic acid.

Table 2. Antifungal activity of representatives of the genus *Streptomyces* against phytopathogens

| Genera/species | Phytopathogene | Published |
|-----------------------------------|---|---------------------------|
| <i>Streptomyces</i> sp. | <i>Fusarium</i> sp. | Nazari et al. (2023) |
| | <i>Rhizoctonia</i> sp. | |
| | <i>Sclerotinia</i> sp. | |
| | <i>Pythium</i> sp. | |
| | <i>Fusarium</i> sp. | Djemounai et al. (2023) |
| <i>S. bellus</i> | <i>Fusarium equiseti</i> | Aallam et al. (2022) |
| <i>S. saprophyticus</i> | <i>Fusarium fujikuroi</i> | |
| <i>Streptomyces</i> sp. | <i>Fusarium oxysporum</i> | Kawicha et al. (2023) |
| <i>Streptomyces viridosporus</i> | <i>Fusarium oxysporum</i> | El Sharkawy et al. (2022) |
| <i>Streptomyces</i> sp. | <i>Rhizoctonia cerealis</i> | Zhu et al. (2023) |
| | <i>Rhizoctonia solani</i> | |
| <i>Streptomyces atratus</i> | <i>Sclerotinia sclerotiorum</i> | Elsafie and Camele (2022) |
| <i>Streptomyces tauricus</i> XF | <i>Puccinia striiformis</i> f. sp. <i>tritici</i> | Jia et al. (2023) |
| | <i>Fusarium oxysporum</i> | |
| <i>Streptomyces roseocinereus</i> | <i>Botrytis cinerea</i> | Chouyia et al. (2020) |
| MS1B15 | <i>Phytophthora cactorum</i> | |
| | <i>Phytophthora cryptogea</i> | |

They describe direct ways as mechanisms in which plants are directly supplied with nutrients produced by microorganisms or mechanisms in which these compounds aid in better nutrient uptake. Therefore, Javed et al. (2021) and Bouizgarne (2022) include the production of siderophores, phytohormones, fixation of atmospheric nitrogen and dissolution of phosphates or minerals in the category of direct mechanisms, thus changing them into a form acceptable to plants.

Bhatti et al. (2017) report that interactions of actinomycetes with non-pathogenic microorganisms also positively affect plant growth. As an example, they cite the ability of actinomycetes to stimulate the formation of mycorrhizal relationships between plants and mycorrhizal filamentous fungi. The positive relationship between actinomycetes and mycorrhizal fungi was confirmed, for example, by Chen et al. (2020), El-Sharkawy et al. (2022) and Wang et al. (2024), who evaluated the species *Streptomyces tricolor*, *S. tendae*, *S. viridosporus* and the genus *Frankia* spp. as mycorrhiza-promoting actinomycetes.

According to several authors, enzymes produced by microorganisms, such as dehydrogenases, β -glucosidases, amidases, phosphatases, aryl sulfatases, and FDA (fluorescein diacetate) hydrolysis, are important in terms of evaluating soil quality and health. According to Chettri et al. (2021), these enzymes are mainly of microbial origin and, together with Neemisha and Sharma (2022), report that enzymes respond quickly and well ahead of other indicators to various anthropogenic interventions in the soil environment. These are mainly enzymes that play a key role in soil processes, in the case of decomposition of organic substrate in the soil, in stabilising the soil structure and in ensuring the natural cycle of nutrients.

According to Bhatti et al. (2017), the production of soil enzymes not only aids the natural nutrient cycle and humus formation but also has a so-called "buffering" ability in the soil, which is a reflection of the conversion of high-molecular organic pollutants in polluted soils and the reduction of pathogens. By producing mainly specific extracellular enzymes, actinomycetes contribute not only to the stability of the basic chemical-physical condi-

tions of the soil, but also increase its production capacity and improve its individual parameters evaluated in relation to the attributes of soil quality and health.

Also, according to many other authors (Javed et al., 2021; Devi et al., 2022; Hungund et al., 2022; Katti et al., 2022; Kontro et al., 2022), actinomycetes, in particular, are active producers of various hydrolases and cellulases. Das et al. (2021), Hungund et al. (2022), Kontro et al. (2022), and Kimeklis et al. (2023) confirm that the enzymes necessary for the decomposition of cellulose in the soil are mainly produced by representatives of the genus *Streptomyces*. Their effect on the higher production of this enzyme (including the enzymes alkaline phosphatase and urease) in the soil environment has been demonstrated, for example, by Ali et al. (2021b), in the case of the *Streptomyces pactum* Act isolate 12. Based on molecular analyses, Kimeklis et al. (2023) found a total of 60 different genes in actinomycetes, encoding cellulolytic enzymes from the glycoside hydrolases group. Hungund et al. (2022) report in their publication that the species *Streptomyces reticuli* has approximately 456 genes that encode enzymes necessary for the degradation of cellulose and other carbohydrates. Pacios-Michelena et al. (2021), in turn, report the 172 genes present in the case of *Streptomyces coelicolor*, which are responsible for the production of hydrolases, chitinases, cellulases, lipases, nucleases and proteases. Castañeda-Cisneros et al. (2020) confirmed the production of endoglucanase and xylanase in agricultural soils in *Streptomyces flavogriseus*, *S. virginiae* and *S. griseoaurantiacus*. The production of both enzymes was also demonstrated by Vargas Hoyos et al. (2021) with the strain *Streptomyces rishiriensis* 3AS4. Gong et al. (2020), Das et al. (2021) and Kontro et al. (2022) also list other representatives of the genera *Actinomadura*, *Micromonospora*, *Microbispora*, *Kitasatospora*, *Thermomonospora*, *Thermobispora*, *Actinoplanes*, *Thermobifida* and *Streptosporangium* as cellulolytic actinomycetes.

In the case of the decomposition of other biopolymers, e.g. starch, actinomycetes also produce other hydrolytic enzymes, such as amylases. Hungund et al. (2022) confirmed this with the species *Streptomyces*

erumpens. Das et al. (2021) also report representatives of the genera *Micromonospora* and *Microbispora*, and Kontro et al. (2022) also mention the species *Thermomonospora curvata*.

Barka et al. (2016) and Das et al. (2021) report the species *Streptomyces antibioticus*, *S. aureofaciens*, *S. lividans*, *S. plicatus*, *S. halstedii* AJ-7 and *S. lydicus* WYEC108 as producers of chitinase. This enzyme is used by actinomycetes in the fight against pathogenic microscopic filamentous fungi, as it can disrupt their cell wall (Al-Quwaie, 2024). Nazari et al. (2023) report that chitinase also helps representatives of the genus *Streptomyces* in biocontrol activity against nematodes such as *Meloidogyne incognita* by 82.13 to 86.96% and in its larval stage by 97 to 100%. The bioinsecticidal potential of actinomycetes against *M. incognita* was also demonstrated in their study by Atif et al. (2023).

Streptomyces also confirm good activity in the case of the breakdown of proteins and amino acids, nucleoproteins, urea, pectins and other substances that are more difficult to degrade, especially classified as xenobiotics. Hungund et al. (2022) and Kontro et al. (2022) state that the strain *Streptomyces* sp. Al-Dhabi-82 is a significant producer of alkaline protease, which is often produced by species of the genus *Streptomyces*, but it also includes representatives of the genus *Nocardia* among the producers of this enzyme. A frequently evaluated and produced enzyme in the soil by streptomyces is also the enzyme phosphatase, which is important in terms of the sufficient availability of phosphorus for plants. Fathalla (2020) reports urease production, representatives of the genus *Frankia* and in the strain *Streptomyces pactum* Act12, confirmed by Ali et al. (2021b) and Qi et al. (2022). Devi et al. (2022), on the other hand, also list actinomycetes as pectinase producers, which is also confirmed in their work by Das et al. (2021) in the species *Streptomyces lydicus* and *Nocardiopsis prasina*.

According to Dangar et al. (2022), actinomycetes produce a unique set of enzymes with the ability to break down xenobiotics in soil efficiently. Shoba et al. (2022) confirm their ability to biodegrade and bioremediate de-

pending on environmental conditions, detoxifying the soil from substances such as organochlorines, triazines, sulfonyleureases, carbamates or organophosphates. Dangar et al. (2022) describe in their work actinomycetes, which are capable of degrading pesticides, among other pollutants. They list representatives such as *Frankia alni* ACN149 (biodegradation of herbicides with atrazine), *Streptomyces aureus* HP-S-01 (biodegradation of insecticides with deltamethrin), *Streptomyces diastaticus* (biodegradation of insecticides with cypermethrin), *Streptomyces* sp. AC1-6 (biodegradation of insecticides with diazinon), *Streptomyces* sp. AH-B (biodegradation of the herbicide Quinclorac). Prajapati et al. (2024) state that many indirect and direct mechanisms of action of representatives of the genus *Streptomyces* contribute to mitigating the negative impact of heavy metals on crops, as they change the process of mobilisation and transfer of metals to different parts of plants. Ali et al. (2021a) confirmed in their study the reduction of available zinc by biosorption in the soil after application of the strain of *Streptomyces pactum* Act 12, as well as lead by the isolate of *Streptomyces pactum* Act 12. For both elements, the authors also describe an improvement in the phytoextraction of heavy metals by cultivated crops. They also describe the effect of actinomycetes on the activity of antioxidant enzymes and the content of malondialdehyde in plants, which confirms the improvement of plant tolerance to stress caused by the presence of heavy metals. This finding correlates with the work of Xu et al. (2023), who investigated the efficacy of the *Streptomyces pactum* Act 12 strain together with the *Streptomyces rochei* D74 strain during phytoremediation. They found that these strains were most effective when applied in combination with organic fertilisers, when they were able to reduce the amount of cadmium in the underground and above-ground parts of the wheat by 56.39%. The strain of *Streptomyces pactum* Act 12 and its effectiveness in the bioremediation of heavy metals such as zinc, cadmium, copper, and lead are also reported in their work by Nazari et al. (2023). Other actinomycetes with the ability to decontaminate soils include *Streptomyces acidiscabies* E13, *S. corchorusii* CASL5, or *Streptomyces*

sp. MC1. Lawal et al. (2021) also describe actinomycetes from the genus *Frankia*, which can remove heavy metals from the environment in the process of bioabsorption. Heavy metals react with negatively charged groups on the cell wall of these microorganisms and bind to them through processes such as complexation, chelation, ion exchange and precipitation. The authors report that combining nitrogen-fixing bacteria with phytoextraction plants that can absorb metals could potentially increase the efficiency of removing heavy metals from the soil. The species of the genus *Frankia* are also mentioned about heavy metals by Nouioui et al. (2023), who isolated a new strain of *Frankia colletiae* Cc1.17, which is resistant to high concentrations of heavy metals such as Pb^{2+} (4mM), CrO_4^{2-} (0.5 mM), and AsO_4^{3-} (25 mM).

CONCLUSION

The main function of agricultural land is to support plants, animals and soil microorganisms. However, when managing the soil, it is necessary to preserve not only its production properties, but also the quality of other components of the environment, especially water and air. This sustainable method of soil management must be evaluated on the basis of indicators of soil quality and health attributes. In addition to physical and chemical indicators, it is therefore necessary to evaluate biological indicators. Within them, indicators about the abundance and microbial activity in the soil (oligotrophic and nitrogenous bacteria, microscopic filamentous fungi, microbial biomass carbon, potentially mineralizable nitrogen, growth rate, respiration, cellulose decomposition) and soil indicators of microbiological diversity (overall microbiome, habitat diversity and organism diversity indices) are monitored. Recently, actinomycetes, particularly streptomycetes, have been reported as important indicators of soil quality and health. Their increased presence and activity in the soil may indicate the presence of more difficult-to-decompose organic matter (including xenobiotics), a dry and alkaline environment. On the other hand, increased production of cellulases, hydrolases, and bioactive metabolites, including phytohormones, nitrogen fixation, can positively affect the production,

defence, and phytoremediation capacity of plants. They signal the presence of a functionally active and stable microbial community that promotes plant growth, suppresses pathogens, and contributes to biochemical cycling. A balanced and diverse community of streptomycetes correlates with a healthy rhizosphere and stability of the soil microbiota. Therefore, future research should focus on establishing standardized, validated, and widely applicable methodologies for the assessment of actinomycete based soil health indicators, allowing robust comparison among diverse environmental and agricultural conditions.

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