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SOIL FUNCTIONS AND THE ROLE OF BIOLOGICAL ACTIVITIES

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Despite soil is a thin layer covering terrestrial Earth surface, it carries out functions that are essential for the terrestrial life forms and these functions are mainly conducted by soil microorganisms, such as fungi and bacteria. They live in a complex, structured and peculiar environment. Microbial diversity is huge and soil is considered the most biodiverse ecosystem on Earth because a handful of soil can contain thousands of millions microbial cells. Despite the high microbial biomass only less than 1% of the available space is occupied by soil microorganisms because most of the available microenvironments show conditions hostile to microbial life. The application of molecular techniques has markedly improved the knowledge of the microbial life and activity in soil. In particular, the microbial species inhabiting soil can be detected whereas the expression of genes is still a technical challenge. Gross rates of nutrient transformations can be determined by using labelled compounds with positive implications on the evaluation of soil nutrient dynamics, including availability for plants.

Key words: soil quality; functional redundancy; amplicon sequencing; N reactions; stable isotope probes.
Parole chiave: qualità del suolo; ridondanza funzionale; sequenziamento; metagenoma; sonde con isotopi stabili.

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1. Introduction

The many important functions of soil can be summarized in five categories: 1) it is the medium for plant growth being the physical support, providing air and water to roots, attenuating temperature changes, protecting against toxins and providing nutrients; 2) it regulates the fate of waters in the hydrological systems; 3) it recycles organic wastes; 4) it is the habitat of soil organisms; 5) it is an engineering medium because it can provide building material and the foundations for houses, roads, airports etc. Therefore, despite soil is a thin layer covering the terrestrial Earth surface it supports all terrestrial life forms. The importance of

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soil for the life is well summarized by the definition of soil quality "The capacity of a soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality and promote plant and animal health" proposed by Parkin and Doran (1994). This definition encompasses: 1) productivity, the ability of soil to enhance plant and biological productivity; 2) environmental quality, the ability of soil to attenuate environmental contaminants, pathogens, and offsite damage; 3) animal health, the interrelationships between soil quality and plant, animal, and human health. Nowadays, the research on soil is also focused on its role in climate change because soil can mitigate the increase of carbon dioxide in the atmosphere by storing organic C and it can release greenhouse gases, such as carbon dioxide, nitrogen oxides and methane if its use is not properly managed.

Several attempts have tried to evaluate soil quality by determining a minimum data set which included few biological, chemical and physical properties. For example, Andrews *et al.* (2004) proposed to integrate ten indicators (water-stable aggregates, bulk density, microbial biomass C, potentially mineralizable N, plant-available water-holding capacity, electrical conductivity, sodium adsorption ratio, pH and total organic C) to evaluate soil quality. There is no agreement about which soil properties should be measured to assess soil quality. It is not possible to determine everything. However, it is well established that biological properties are more sensitive than chemical and physical properties to changes in soil quality (Schloter *et al.*, 2018). In addition, they drive most of soil ecosystem services (Nannipieri *et al.*, 2003) and for this reason this is one of the hot topics in soil science studies.

This brief review will discuss the peculiarity of soil as a biological system and the role of soil biological activities in driving soil functions. The great advances in the knowledge of soil as a biological system and of the role of soil biological functions occurred after the use of molecular techniques based on the extraction and characterization of nucleic acids and proteins. The collaboration of soil biologists, including soil microbiologists, with soil chemists and soil biochemists, like myself, has solved technical challenges involved in studies of these soil molecules. It is not possible here to have an exhaustive review due to the complexity and vastness of the treated matter, which exceeds the limits of a synthetic review. To have a more detailed discussion of the issue I suggest the reader to consult the many cited reviews.

2. Soil as a biological system

Soil biota include microorganisms (bacteria, actinomycetes, archaea, fungi, algae, protozoa and nematodes) microfauna, mesofauna and macrofauna. The size is important because soil is a structured system with soil particles differing in shape and size and linked or separated by pores differing for their size and this may

explain the spatial separation of soil organisms, because: i) microarthropds can only inhabit macropores; ii) nematodes can also live in intermacroaggregate pores; iii) protozoa, small nematode and fungi can also be present in intramacroaggregate or intremicroaggregate pores; iv) whereas intramicroaggregate pores can only be occupied by bacteria and virus (Elliott and Coleman, 1988). Indeed, the pore occupancy depends on the organism size; for example, bacterial size is a few micrometres, that of fungi is less than 100 μm whereas that of Acari and Collembola ranges from 100 μm to 2 mm. The occupation of different pores can have important effects on soil organisms because, for example, bacteria inhabiting intramicroaggregates pores escape protozoa predation.

Microbial biomass, which is the contribution of biomasses of fungi, bacteria, archaea and protozoa, prevails over the biomass due the other soil organisms (Nannipieri, 2020). Among the soil microorganisms, bacteria and fungi largely prevail being their biomass 10^2 to 10^4 fold higher than biomass of archaea, protists and viruses (Dini-Andreote and Van Elsas, 2019). However, only less than 1% of the available space is occupied by soil microorganisms likely because most of the soil microenvironments are hostile to microbial life due to many abiotic and biotic stresses (lack of nutrients, presence of toxic elements or compounds, etc); in addition, less than 5% of microbial biomass is composed by active taxa (Dini-Andreote and Van Elsas, 2019). Microbial activity occurs if energy sources are available or if temperature and soil moisture turn to favorable conditions

Microbial diversity is huge and soil is considered the most biodiverse ecosystem on Earth because a handful of soil can contain thousands of millions microbial cells (Dini-Andreote and Van Elsas, 2019). The abundances and diversity of soil microorganisms vary markedly across soil types but there is the dominance of a few groups. For example, 500 bacterial taxa (representing 2% of the total detected taxa) represented about 40% of bacterial diversity in different soils across the globe (Dini-Andreote and Van Elsas, 2019). Some of the ubiquitous and dominant phylotypes included Alphaproteobacteria (*Bradyrhizobium* spp*, Sphingomonas* sp, *Rhodoplanes* sp, *Devosia* sp, and *Kaistobacter* sp), Betaproteobacteria (*Methylibium* sp and *Ramlibacte*), Actinobacteria (*Streptomyce* ssp, *Salinbacterium* sp and *Mycobacterium* sp), Acidobacteria (*Candidatus* sp, and *Salibacter*) and Plancttomycetes. However, most of the extracted 16S RNA sequences are unknown because on average less than 18% of the identified phylotypes matched to an available genome at the 97% 16S rRNA sequence similarity level, and 40% at the 90% 16S rRNA sequence similarity level (Dini-Andreote and Van Elsas, 2019).

Viruses are present in soil but they have been less studied than soil organisms; agricultural practices can affect both abundance and diversity of soil viruses, which are mainly bacteriophages, which can infect either pathogenic soil bacteria or beneficial bacteria, such as rhizobia (Nannipieri, 2020). However, the role of virus in biological processes and survival of organisms in soil is poorly known.

Another peculiar aspect of soil as a biological system is the ability of surface-reactive particles to adsorb important biological molecules, such as nucleic acids and proteins, and protect them from the degradation of the heterotrophic soil microbiome (Nannipieri, 2020). This means that soil can have active extracellular enzymes or genetic material independent of the soil microbiome. Thus these stabilized enzymes can catalyze reactions even if the soil microbiome is largely inactive and competent bacterial cells can take up extracellular and stabilized DNA giving the bacterial transformation, that is the incorporation of the genes of the extracellular DNA in the genome of the host bacterial cell (Nannipieri, 2020).

3. Biological functions

The main microbiological functions are summarized in Table 1. The reported processes are the results of many reactions. Many different microbial species can carry out several soil metabolic processes and thus any soil is characterized by functional redundancy; for example, the taxonomical variability was much higher than the functional variability in bacterial communities degrading straws (Bao *et al.*, 2020). For this reason, the loss of microbial diversity cannot affect processes, such as C and N mineralization (Nannipieri, 2020) until a certain threshold value of microbial diversity is reached (Juarez *et al.*, 2013). Generally processes, such as nitrification, carried out by only some microbial species are affected by the decrease in microbial diversity (Nannipieri, 2020). For example, microbial diversity reduced by heavy metal pollution did not affect soil organic mineralization, a process carried out by many different microbial species, but affected the simazine degradation, which is carried out by a limited number of soil microbial species (Singh *et al.*, 2014). The determination of labelled carbon dioxide is used to measure the decomposition of the labelled organic C compound and to distinguish such degradation from the mineralization of soil organic matter; this method determines the final product (carbon dioxide) but ignores the sequence and type of enzymes responsible for degradation of the organic C compound (Nannipieri, 2020). Future research should study the effects of changes in microbial diversity not only on the rate of the produced carbon dioxide but also on the activities of the several enzyme activities which are responsible of the oxidation of the labelled compound in soil.

Interactions between microbes and between microbes and plants can markedly affect soil functions. Microorganisms inhabiting soil around the rhizosphere can have beneficial, negative and no effects on plants. Microbial inoculation with beneficial microorganisms is nowadays the best approach to modify soil microbiome to produce beneficial effects on plants; bacteria and mycorrhizae are often used as inoculants. Due to the limited space I shall only discuss the main challenges due to the use of bacterial inoculants. Beneficial bacteria are classified

Table 1 - Main processes carried out by soil microbiome.

Oxidation of organic matter including xenobiotics
Humification (Largely unknown)
N transformations
P transformations
S transformations
Micronutrients transformations
Interactions with plants
Interactions with soil biota

as "biocontrol plant growth-promoting bacteria" (Biocontrol-PGPB) and "plant growth-promoting bacteria" (PGPB) (de-Bashan *et al.*, 2020). Usually bacterial inoculants are used to promote plant growth, biocontrol pathogens or for soil bioremediation. Often the performance of PGPB strains under field conditions gives contradictory and inconsistent results because not all the following issues have been considered (Cassan *et al.*, 2020; Gamalero and Glick, 2019): i) knowledge of the PGPB survival in the soil-plant system under study with determination of the fate of the inoculated bacteria; this requires to understand if the inoculant will be able to compete with the indigenous microbiome of the plant-soil system; another important aspect is the choice of the proper plant strain capable of interacting with the inoculant; ii) use of the proper formulation to deliver the inoculant so as to allow its activity in the soil-plant system under study; iii) complete analysis of the inoculant's physiological traits responsible for the positive effects on the plant. To generalize the obtained results it is important to repeat at least once the inoculation experiments and to track or monitor the microbial inoculant. If molecular tools are not available it is possible to have an indirect monitoring of the inoculant by using some of the easy classical methods (de-Bashan *et al.*, 2020).

Interactions between microorganisms have been extensively studied (Van Elsas *et al.*, 2019) and they occur through molecular signals, such as those between bacterial cells, that is the quorum sensing (QS), discovered in 1980s and causing the regulation of several bacterial processes, such as symbiosis, virulence, competence for transformation, conjugation, antibiotic production, motility, sporulation and biofilm formation (Van Elsas *et al.*, 2019). These signals are important in assemblage of bacterial cells because cells of species with specific QS signals can exclude cells of species with anti-QS signaling traits (Van Elsas *et al.*, 2019). However, an example of how complex the interactions among

plants and soil microorganisms are and how they involve several players is given by the microbial loop (Bonkowsky and Clarholm, 2021). Root exudates released from root tips can stimulate the growth of bacteria capable of mining N from soil organic matter because root exudates are generally C-rich compounds. The bacterial growth stimulates the activity of protozoa grazing bacteria and this causes the decrease in bacterial abundance with release of ammonium-N because the C/N ratio of protozoa cells is higher than that of bacterial cells. The released ammonium is taken up by the plant and thus the microbial loop shifts the competition for N between plants and bacteria in favor of plants.

4. Technical improvements for measuring soil functions and advances on the knowledge of soil microbial functions

As already mentioned the use of molecular technique has revolutionized the knowledge on soil microbiological functions. An example of these advances is the knowledge progress about soil nitrification. The conversion of ammonia to nitrite is carried out in soil not only by ammonia oxidizing bacteria (AOB), as previously believed, but also by ammonia oxidizing archaea (AOA); both contain the *amo* genes responsible for the synthesis of the enzyme converting ammonium to hydroxylamine. AOA can be dominant in agricultural soils especially if ammonium is gradually released by N mineralization; the addition of N fertilizers can stimulate the growth of AOB due to the rapid increase of soil ammonium (Nardi *et al*., 2020). Another important difference between AOA and AOB is that the production of N_2O (greenhouse gas with 298 times Global Warming Potential than CO_2 and natural catalyst of stratospheric ozone degradation) is higher in the nitrification processes carried out by AOB. The process of oxidation of hydroxylamine to nitrite occurs through the formation of NO and not, as long believed through the oxidation of hydroxylamine directly to nitrite; the formation of NO does not require oxygen and it is coupled to the formation of N_2O (Nardi e*t al*., 2020). The oxidation of nitrite to nitrate is carried out by nitrite oxidizing bacteria (NOB). However, in 2015 it was discovered that strains of *Nitrosospira* (also present in soil) had the enzymes for the complete oxidation of ammonia to nitrate (Comammox nitrification) (Nardi *et al*., 2020). In addition to AOA, AOB, NOB and the Comammox, fungi and heterotrophic bacteria can produce nitrate in soil by heterotrophic nitrification by using ammonium or organic N as substrate. The AMO-like enzyme of some heterotrophic nitrifiers uses ammonium as the substrate and not ammonia as AOA and AOB (Nardi et al 2020). Some heterotrophic nitrifiers, mainly fungi, can oxidize organic N compounds, such as amines or amides, to intermediates with nitroso (R-NO) and nitro ($R\text{-}NO_2$) groups and then to nitrate. The model set up by Müller *et al*., (2007) and based on the determination of the gross

N rates can determine both autotrophic and heterotrophic nitrification. Finally to make the picture of soil nitrification in soil more complex, Kuenen (2008) discovered the Anammox process, the anaerobic oxidation of ammonium by bacteria using nitrite as an electron acceptor with production of N_2 and oxidation of nitrite to nitrate.

The amplicon sequencing or metagenome techniques determine the microbial taxa responsible for soil microbial reactions. However, these studies suffer of the following two drawbacks, often ignored: i) it is assumed that the detected microbial species carry out in soil the same functions observed *in vitro*; ii) the presence of functional genes is often taken as a proxy that the relative function potentially occurs in the soil where these genes are detected without determining the gene expression or relating this presence to the measurement of the target activity (Nannipieri, 2020). As mentioned above, most of the microbial species inhabiting soil are inactive and rare but not dominant species can be responsible for the determined activity when expression of genes is related to the measured activity (Jiang *et al.*, 2019; Wei *et al.*, 2019). It is well established that metagenome studies should be combined with proteomic analyses to get insights into soil functions, because proteins are the final expression of each genome. Unfortunately, soil proteomics still shows challenges and pitfalls, such as it is not technically possible to determine all expressed proteins and it is not possible to extract all expressed proteins from soil (Nannipieri, 2020).

The use of labelled (for example, with ^{14}C or enriched with ^{15}N) compounds or the determination of changes in the abundances of stable isotopes (for example, ^{13}C) is nowadays the best approach to quantify nutrient transformations in the soil-plant system (Nannipieri, 2020). According to the holistic approach, the system is partitioned into pools (for example, microbial biomass C, microbial biomass N) with a functional meaning, and fluxes between these pools can represent abiotic processes (for example, nitrate leaching or ammonia volatilization) or biotic transformations (for example, nitrification, mineralization, etc). In this way the distribution of the labelled compound can be monitored through the different pools. In addition, it is possible to discriminate the added nutrient from that already present in soil; for example, the fate of the ^{15}N enriched fertilizer is distinguished from the fate of the native soil N. Both N immobilization and N mineralization play a crucial role in affecting the amount of N available to plants but unfortunately the present techniques do not allow the determination of organic N pools with different turnover. The organic N pool cycling faster contribute more to the N mineralization-immobilization than the organic N pool with a slower turnover.

The stable isotope probing (SIP) is the technique that combines the holistic approach with molecular methods because it determines the active microbial populations using the substrates labelled with stable isotopes (usually ^{13}C or ^{15}N) (Nannipieri, 2020). Indeed the heavy (labeled) DNA of the active microbial populations is separated from the light (unlabeled) DNA of microbial populations

not using the added compound to soil. This technique can give insights not only into the stimulation of rare and dominant operational taxonomic units (OTUs) using the labelled compound but also into microbial taxa indirectly affected by the added compound by analyzing changes in the abundance of unlabeled OTUs compared to those of the control soil (only water added) (Bao *et al.*, 2019). There are two main drawbacks about the SIP technique: i) the sensitivity of DNA-SIP is less than that of phospholipid fatty acids (PLFA)-SIP because the former requires cell replication for incorporation and thus incubation times longer than those required for PLFA; ii) the cross-feeding, that is the labelling of microorganisms not directly involved in the substrate utilization but using labelled metabolites produced by the users (Nannipieri, 2020).

5. Conclusions

The past two decades have witnessed the development of novel techniques and large-scale projects that have revolutionized our understanding of soil as a biological system. Techniques such the SIP determine the microbial populations using compounds added to soil and the effects of these microbial users on those not involved in the use of the compound. Gross rates of nutrient transformations are determined by using labelled compounds with positive implications about evaluating the dynamic, included the plant availability, of nutrients in soil. Despite these advances several aspects of soil as a biological system are still unknown. Technical challenges concern the visualization of active and inactive microbial species and extracellular stabilized proteins and nucleic acids in the soil matrix. Detection but not expression of genes in soil is nowadays possible. Further research should address: i) the determination of proteins as final expression of genes in soil; ii) the set up of methods to determine organic pools with different turnover so as to improve the tracking of nutrients in soil; iii) the study of forest soils by applying the above mentioned techniques not only because they are storing large quantities of organic C and the relative plant-soil systems are important for decreasing the atmospheric concentration of CO_2, but also because these soils carry out crucial ecosystem services.

RIASSUNTO

Le funzioni del suolo e il ruolo delle attività biologiche

Nonostante il suolo sia uno strato sottile che ricopre la superficie terrestre, esso svolge funzioni essenziali per le forme di vita terrestri, principalmente grazie all'attività dei microrganismi del suolo, come funghi e batteri, che vivono in un ambiente complesso, strutturato e peculiare. La diversità microbica è enorme e il suolo è considerato l'ecosistema più ricco di biodiversità sulla Terra perché una manciata di suolo può contenere migliaia di milioni di cellule microbiche. Nonostante l'elevata biomassa microbica solo meno dell'1% dello spazio disponibile è occupato da microrganismi del suolo perché la maggior parte dei microambienti disponibili presenta condizioni ostili per la vita

microbica. L'applicazione di tecniche molecolari ha notevolmente migliorato la conoscenza della vita e dell'attività microbica nel suolo. In particolare, le specie microbiche che abitano il suolo possono essere rilevate mentre l'espressione dei geni rappresenta ancora una sfida tecnica. I tassi lordi delle trasformazioni dei nutrienti possono essere determinati utilizzando composti marcati con implicazioni positive per la valutazione della dinamica, inclusa la disponibilità per le piante, dei nutrienti nel suolo.

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