Mycorrhizal fungi: the symbiotic friends of plants

Sir: I overheard some biologists mumbling about AM and P: were they talking about morning and afternoon?

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Storyline

Plants can do a terrific process called photosynthesis:

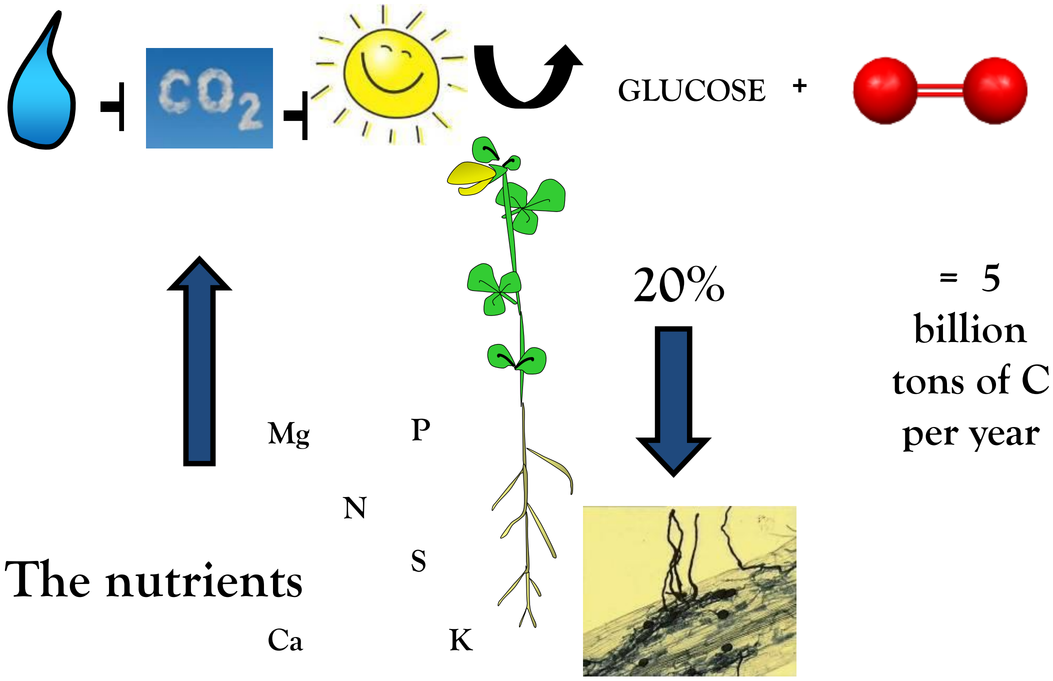


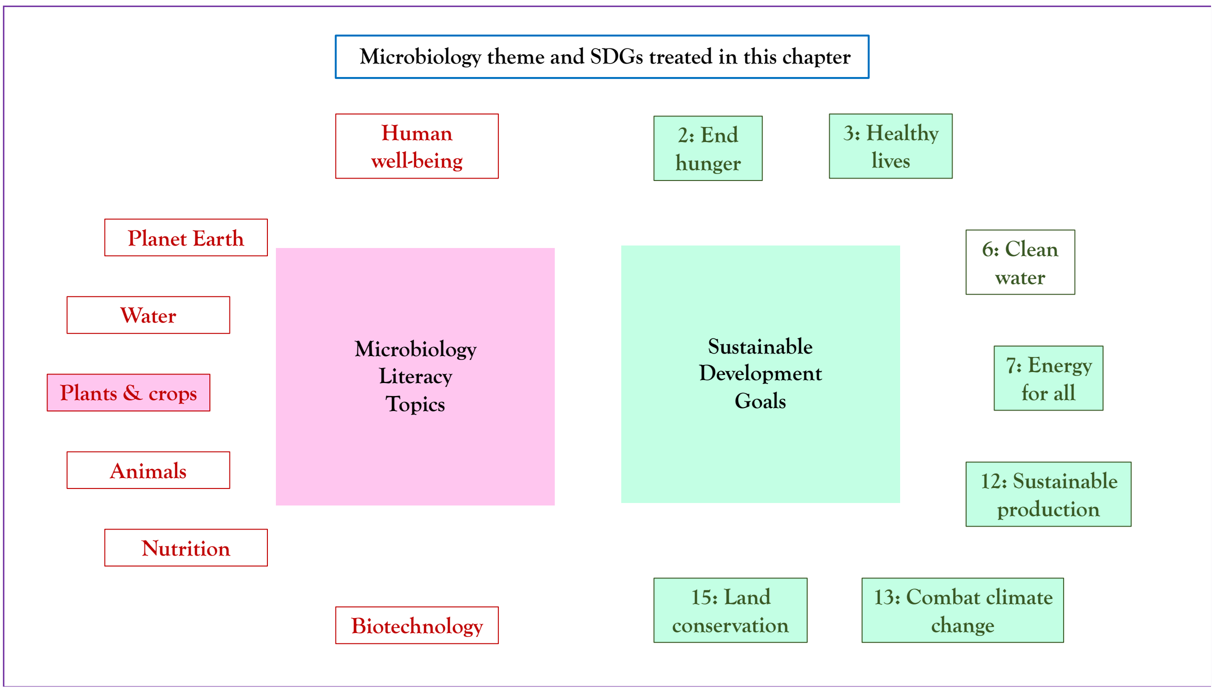
Fig. 1. For the photosynthetic process, plants need not only water and carbon dioxide, but also mineral nutrients that they must take up from the soil. Mycorrhizal fungi that live in their roots, as shown in the little box at the bottom, help them in a very efficient way. On the other hand, plants release carbon in the soil, which is directly used by mycorrhizal fungi. Photosynthesis creates glucose, which feeds the plant and its mycorrhizal fungi, and oxygen, which we, other animals and plants need for respiration.

During this process, plants take the energy from sunlight and use it to convert carbon dioxide and water into food for them (to grow, to produce flowers, seeds, and new little plants) and for all of us. In addition, plants release oxygen, which is indispensable for us. So most life in the planet depends on plant photosynthesis (microbes also carry out photosynthesis, and yet other microbes can grow using chemical energy instead of energy from the sun). However, what is less known, is that, in order to be healthy and to do an excellent photosynthesis, plants also require many nutrients, i.e. minerals coming from the soil, in order to accomplish what we call *the mineral nutrition* of the plants. To be healthy and fertile, soils must contain a large supply of nutrients, which are taken up by plants when they absorb water. *Since animals feed on plants, and we feed on plants and animals, soil is the ultimate source of mineral nutrients for all living beings.*

Minerals get into the soil in many different ways: nitrogen is produced from decomposed animal waste and dead plants, thanks to saprotrophic microbes, or from the atmosphere, thanks to special bacteria which convert it into ammonium that plants can use. Other nutrients such as phosphorus, potassium, calcium, and magnesium "weather" out from inorganic sources such as rocks, while others like sulphur come from both organic and inorganic sources, including the atmosphere. Unfortunately, all these nutrients are present in very low quantities in soils, leaving plants always starved for these precious nutrients. But luckily, plants are not alone in facing this job: in addition to the *rhizobia, the bacteria which fix the atmospheric nitrogen*, plants are helped by a multitude of fungi (Fig.1, which live in symbiosis with the roots of more than 90% of land plants.

Most of the crops we eat (rice, wheat, tomatoes, potatoes, peppers, carrots, as well as apples, peaches, oranges and cherries) host microscopic fungi called *arbuscular mycorrhizal fungi* (AM fungi), which intimately colonize their root cells. Many of the trees living in the forests, from pines to oaks, willows and beeches, host other fungi that we call *ectomycorrizal fungi* (ECM fungi). Unlike the AM fungi, some of these ECMs produce big fruiting bodies that you can see when you walk in the forests. But also heathers and orchids are helped by their own symbiotic fungi. All these mycorrhizal fungi explore the soil with their minute hyphae and take up minerals: entering in an intimate contact with their host plant, they release the precious minerals to the plants. But the mycorrhizal fungi not only support the plants as bio-fertilizers, they also give their green hosts protection against pathogenic microbes. In return, the plant rewards its symbiotic fungus with a good quantity of organic carbon (which is the product of the photosynthesis). A pervasive example of excellent cooperation between different organisms.

The Microbiology and Societal Context



The microbiology: microbially-driven carbon, nitrogen and phosphorus cycle; the role of mycorrhizal fungi in the phosphorus cycle; the role of mycorrhizal fungi in reducing soil nutrient loss; plant microbiota: not only bacteria. *Sustainability issues:* biodiversity conservation; crops and food: the role of mycorrhizal fungi for a more sustainable agriculture.

Mycorrhizal fungi: the Microbiology

1. ***Microbially-driven carbon, nitrogen and phosphorus cycles***. Microorganisms play central and essential roles in nutrient cycles. Thanks to their plastic metabolism, they couple elemental reactions, driving biogeochemical cycles which involve carbon (C), nitrogen (N), phosphorus (P) and sulphur (S). These events ensure the turnover and supply of nutrients that

are essential for plant and crop growth, through the inter-conversion of different forms of nitrogen, sulphur and phosphorus, interlinked with the carbon cycle. Microorganisms are responsible for the degradation of organic matter, which controls the release of plant nutrients, but is also important for the maintenance of soil structure and sustainability of soil quality for plant growth. Microbial activity in soil is also responsible for carbon losses to the atmosphere through respiration and methanogenesis, and microorganisms are required for remediation, through degradation of organic pollutants and immobilisation of heavy metals, providing obvious examples of improving soil quality.

2. ***The role of mycorrhizal fungi in the phosphorus cycle***. The Earth's biological systems have moved around the availability of phosphorus since the beginning of life. DNA – the material of genes that determine heredity, adenosine triphosphate (ATP) that provides the energy needed to drive cellular metabolism, phospholipids that make up cell membranes, all contain phosphate. But phosphorus (P) is present in only minute quantities in the Earth's crust (0.09 wt.%), mostly present in a few carbonate minerals. These rocks represent the P reserves that are exploitable in an economically viable way and that are projected to become exhausted during the next century. In soils, weathering releases P as phosphate from minerals by several processes, such as microbial respiration, which releases CO_2, which in turn increases acidity around degrading organic matter and root hairs. Once P is liberated from minerals during weathering, it becomes part of the circulating soil solution having a concentration of 10-20 ppm. However, phosphate is then quickly sequestered into various soil complexes, limiting its availability to plants and organisms. In principle, therefore, P is a limiting factor for the plant growth.

However, mycorrhizal fungi, i.e. the fungi which live associated with the roots of around 90% of land plants, help plants to acquire P. Mycorrhizal fungi in fact occupy a double niche: in addition to their intimate association with plant roots, they also extend far into the soil, where they produce an extensive absorption network which extends beyond the root depletion zone, i.e. the zone around the root, where the solution of phosphate (and of other minerals) is depleted more quickly than its replenishment.

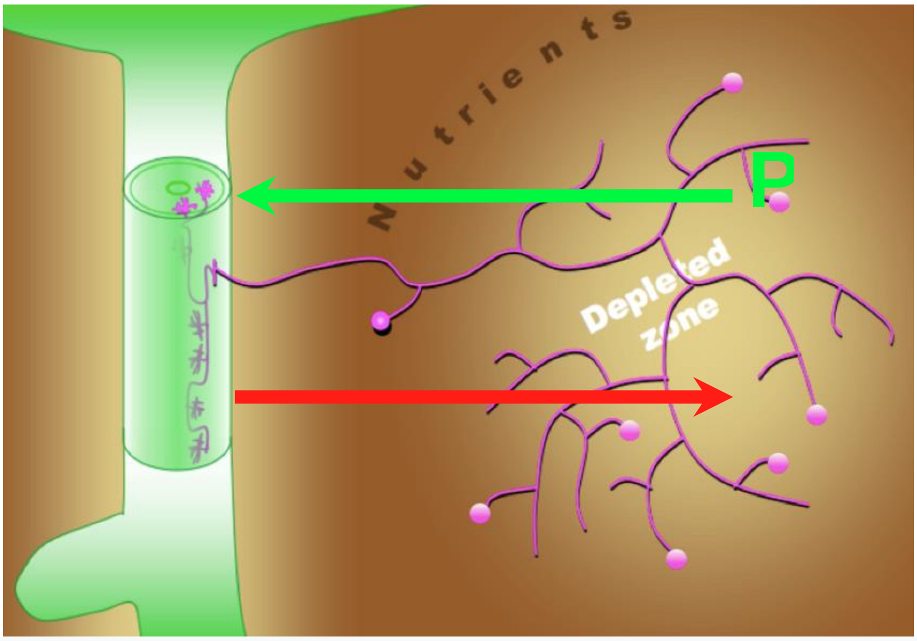


Fig. 2. The AM fungus produces a network of hyphae (in pink) which explore the soil (in brown), going beyond the depletion zone which surrounds the root (in green). The fungus uptakes many minerals, including phosphate (P, green arrow), and translocate them along the hyphae which colonize the roots.

Small little trees (arbuscules) are produced inside the root cells. Here the plant releases the carbon (red arrow) to the fungus.

Thanks to this capacity, mycorrhizal fungi, and in particular AM fungi, have access to a large volume of soil from which they uptake nutrients, including P, zinc, ammonium, nitrate, copper, potassium (K) and S. Up to 90% of plant P and 20% of plant N can be provided by AM fungi, while other mycorrhizal fungi, like those which associate with the roots of forest trees play a more relevant role in the uptake of N. The movement of P into the plant is fuelled by the movement of carbon from the plant to the fungus.

AM fungi are well equipped with specific P transporters, located on their hyphal surface, at the interface with the soil. Once phosphate enters the hyphae, it moves as polyphosphate granules along the hyphae. These penetrate the plant root, forming highly branched structures called arbuscules in cortical cells, and deliver phosphate to the plant root (Fig.2), from which it travels to aboveground parts, reaching epigeous organs probably via the vascular tissues.

3. ***The role of mycorrhizal fungi in reducing soil nutrient loss***. Agriculture and human activities have a deep impact on the mineral cycles: as a consequence of the Green Revolution, fertilizer-based food production and the application of P, along with N, K, and other micronutrients, in commercially available fertilizers boomed in many areas of the planet. The Green Revolution led to prosperity in some countries and exponential growth in global population, but also created environmental damage. A major one is the huge amount of nutrients, which – provided as fertilisers – are lost from soils to which they are applied via leaching and reach the deep layers of the soil and surface waters. Up to 160 kg of nitrogen (N) and 30 kg of P can be lost per hectare due to leaching. N is also lost as nitrous oxide (N_2O), a potent greenhouse gas, with losses up to 143 kg of N per hectare. The role of mycorrhizal fungi, particularly AM fungi, in reducing soil nutrient loss is now emerging. The reduction of nutrient loss by mycorrhizal fungi is accomplished by enhanced nutrient immobilization and probably by altering some nutrient cycling processes, which favour the retention of nutrients in the soil. Figure 3 illustrates how AM fungi reduce the N and P loss, executing a crucial ecological service in agricultural ecosystems.

4. ***The plant microbiota: not only bacteria***. Plants live in ecosystems where they interact with complex microbial communities with which they establish a wide range of relationships. These microbes constitute the so-called 'microbiota', a term coined to describe the diversity of mostly beneficial microbes which colonize all the plant organs, from roots to seeds, from the outer surfaces to the inner tissues. As was the case for the microbes which live in our gut, the knowledge of plant microbiota has required important technical advances, usually identified as 'omics technologies, where informatics, big data and biology meet. The genomic information present in the plant-associated microbiota is defined as "microbiome", also known as the second plant genome. The microbes assist plants, improving their mineral nutrition, impacting some developmental processes (for example root architecture) and increasing their natural immunity. Notwithstanding the differences in the composition of plant and animal microbiota, they share these main functions.

Which are the actors of the plant microbiota? In addition to bacteria, archaea, viruses, insects and oomycetes, fungi represent a relevant component of plant microbiota. A specific name (Mycobiota) has been assigned to these microbes which - as saprotrophic, endophytic or symbiotic microbes - associate with the plant organs. Mycorrhizal fungi and other beneficial fungi dominate in the roots, while Ascomycota and Basidiomycota are very common in leaves.

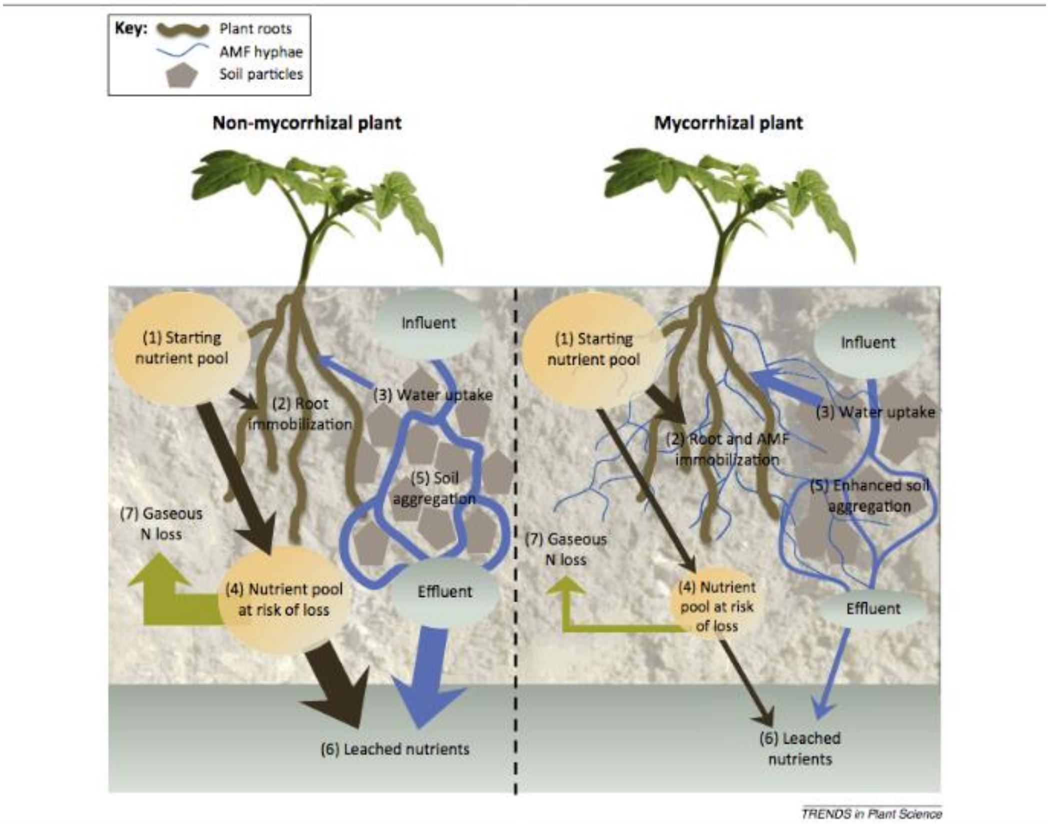


Fig. 3 Impacts of mycorrhizal versus non-mycorrhizal plants on soil nutrient loss pathways. The starting nutrient pool (1) may comprise inorganic and/or organic N- and P-containing compounds. Immobilization of nutrients (2) and water uptake (3) are enhanced when plants are colonized by AM fungi. As a consequence, the pool of nutrients at risk of being leached (4) will be reduced with mycorrhizal plants (6). Simultaneously, AMF can improve soil aggregation (5). Gaseous N loss (7) is enhanced when plants are non-mycorrhizal due to reduced plant N assimilation. (From Cavagnaro et al 2015).

Relevance for Sustainable Development Goals and Grand Challenges

The microbial dimension of acquisition of nutrient uptake by mycorrhizal fungi relates to several SDGs, including Land Conservation; Healthy environments, Healthy life, Combat Climate changes. The following issues - Biodiversity conservation and mycorrhizal fungi; Crops and food: the role of mycorrhizal fungi - are developed in the context of such Grand Challenges.

- **Biodiversity conservation and mycorrhizal fungi.** Mycorrhization is a pervasive process, which is present in a large part of the 340,000 plant species so far identified, and involves around 50,000 fungal species. Mycorrhizal symbioses are present in mostly all ecosystems, from forests to deserts, from meadows to agricultural ecosystems. The success of this symbiosis dates back to the moment in which plants colonized land. Fossil reports reveal that the rhizomes of extant plants dating back to more than 400 million years ago presented fungal structures comparable to those produced by the today AM fungi. The success of mycorrhizas in time and space strongly suggest that mycorrhizal fungi are crucial determinants for plant communities. Several studies have indeed reported that AM fungi enhance plant diversity of grasslands by specifically stimulating the growth of subordinate, often rare plant species.

The underlying mechanisms by which AM fungi promote growth of such mycorrhizaldependent plant species can explain how these fungi promote plant diversity. There is a positive relationship between the mycorrhizal dependency of a plant and the amount of phosphorus released by AM fungi. In addition, interplant carbon transport through a mycorrhizal hyphal network, from one plant to another, is directed towards plant species with the highest mycorrhizal dependency. Plant species with high mycorrhizal dependency, therefore, receive much more resources from AM fungi than plant species with a lower dependency. There are, however, some instances where AM fungi can reduce diversity. This has been observed in tall grass prairies in which the majority of plants had a low mycorrhizal dependency. In conclusion the presence of mycorrhizal fungi is crucial in keeping high the biodiversity of plant communities, a crucial parameter for the sustainability of natural environments.

- **Crops and food in a changing world: the role of mycorrhizal fungi.** Human beings are expected to reach a population size of more than 10 billion in 2050. Providing food that is nutritious and safe for this growing population is one of the greatest challenges for humanity and for science. The climate change scenario with its extreme events is another increasingly challenging task. Some of the latest estimates predict the need to increase agricultural productivity by at least 70% by 2050, by developing more sustainable approaches. The focus is to shift from the intensive agriculture, which is final product of the Green Revolution to a more sustainable agriculture, which, however, is not less productive.

An integrated agriculture, at least in part based on the so-called Microbial Revolution, could in part respond to these requisites. In this context the role of soil biodiversity becomes crucial and plant-growth promoting bacteria, as well as mycorrhizal fungi, become relevant tools in achieving these new goals in a sustainable way. Moreover, agricultural productivity needs to become more resistant and resilient to the new pathogens, which rapidly spread over the continents, as well as to extreme climate events that are increasing in frequency. AM fungi colonize most of the crops which feed the world (Fig.4):

Fig. 4. The plants we eat are mostly AM plants. All the vegetables illustrated, with the exception of the central broccoli, come from plants colonised by AM fungi.

Crop pathogenic fungi and other pests have an enormous public health impact worldwide, since they can be responsible for 20-40 % yield losses per annum, strongly reducing food security at the global level. This requires a better management of crop diseases. Among the more environment-friendly approaches, mycorrhizal fungi offer an unexpected help. Many studies have in fact demonstrated the during early AM formation, there is an activation of plant defence responses, which are explained as a form of plant priming. This kind of protection contributes to the so-called mycorrhiza-induced resistance when AM plants are challenged by biotrophic and necrotrophic pathogens, nematodes, insects and viruses. Due to these AM capacities (not only biofertilisers, but also bioprotectors), many innovative agricultural projects are currently based on the application of AM inocula, often mixed with other beneficial microbes. Many experiments have already demonstrated significant increases in plant productivity. It is impressive to see that, even if AM fungi grow in the hidden organs of the plants – the roots – their beneficial effects are detected on the whole plant, often augmenting the photosynthetic process, as well as improving the seed quality. Given that AM fungi are so far considered obligate biotrophic microbes (they need the plant to accomplish their life cycle), to set up high-level and efficient inocula will be one crucial goal for the agriculture of the future.

Potential Implications for Decisions

1. ***Individual***
   a. To look for markets where vegetables from mycorrhizal plants are sold

2. ***Community policies***
   a. To support at local and national level projects promoting in field experiments with mycorrhizal plants
   b. To support at local and national level projects promoting forest experiments with mycorrhizal trees
   c. To support projects following the whole chain: production of mycorrhizal plants; harvest of final products (tomato for example); evaluation by the consumers

3. ***National policies***
   a. policy regarding the production and the marketing of microbial inocula

Pupil Participation

1. ***Class discussion*** of the issues associated with phosphorus (from eating fish..)

2. ***Exercises*** (could be made at any level, but these are probably secondary education level)

   a. Have the pupils collected mushrooms in the forest?
   b. What do they know about Mycology?
   c. Can they comment Fig. 1?
   d. Looking at the SDGs, how can we change our approach thinking of the ecological role of mycorrhizal fungi?

The Evidence Base, Further Reading and Teaching Aids

websites
https://www.kidsdiscover.com/teacherresources/fungi/

https://bbsrc.ukri.org/documents/mushroom-pdf/
http://www.davidmoore.org.uk/Assets/fungi4schools/GBF_web/Teachers%20notes.htm
https://projects.au.dk/ecofinders/ecosystem-services/nutrient-cycling-in-soil/
https://www.soils4teachers.org/lessons-and-activities/teachers-guide/soils-food-health

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