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Soil Biology of the Canadian Prairies

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Summary

Although some soil microorganisms cause plant diseases, most soil inhabitants are beneficial to crop production and the environment through processes like the fixing and cycling of nitrogen, biological pest control, formation and maintenance of soil structure (tilth), and degradation of agrochemicals and pollutants. This paper discusses the distribution of these organisms in prairie soils and how they are affected by soil and crop management practices. The discussion includes soil fauna and microorganisms, and singles out three groups of microorganisms that are particularly important in crop production: arbuscular mycorrhizal (AM) fungi, dark septate root inhabiting fungi, and rhizobia. The development of healthy diverse faunal and microbial communities in soil can be fostered by using soil management practices or systems like conservation tillage, crop rotation, proper nutrient management and application of organic manures when available.

Major Groups of Soil Organisms

Soil fauna

Soil fauna are a diverse community of soil-dwelling animals. Fauna common in prairie soils include microscopic hair-like worms called nematodes, miniature earthworm-like animals called pot worms or enchytraeids, snails, slugs, springtails, insect larva, beetles, ants, spiders and earthworms. Fauna are functionally classified according to body width: microfauna are < 100 micrometers (µm) wide, mesofauna 100 µm to 2 mm wide, and macrofauna are > 2 mm wide[6]. Nematodes are a good example of diverse microfauna, with species ranging from slightly larger than bacteria (2-3 µm wide) to plant parasitic nematodes that may approach mesofauna in size. Earthworms represent the other extreme, commonly several millimeters wide and up to 200 mm long. Soil fauna demonstrate a variety of feeding habits. These include consumption of organic debri, plant material, or bacteria, fungi or other small soil fauna.

Figure 1: common garden earthworm

Figure 2: insect larva, mite, nematode, 40X Mag.

Figure 3: mite, 40X Mag.

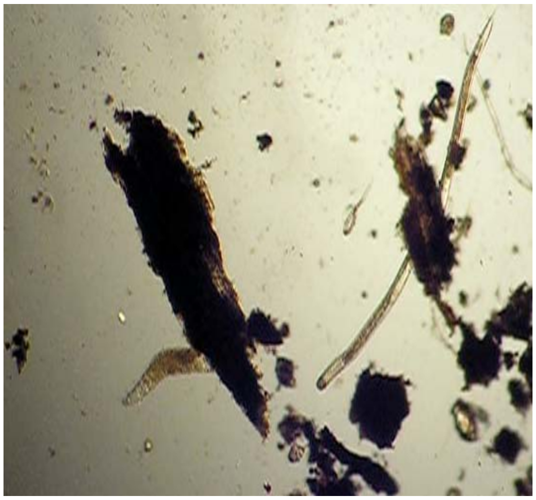

Figure 4: rotifer and nematode, 100X Mag.

Soil microorganisms

Soil microorganisms are those soil organisms that can only be seen with the aid of a microscope. They can be classified in several ways, including morphology, physiology and function. The major morphological groups include bacteria, actinomycetes, fungi, algae and protozoa. Physiologically, they can also be classified according to their energy and carbon sources (Table 1). In relation to function, some microorganisms are N-fixers, ammonia oxidizers, denitrifiers; most are decomposers. Symbiotic microorganisms such as rhizobia bacteria, dark septate endophytic (DSE) and AM fungi have a large impact on crop production. They are particularly important for agriculture.

Table 1. Physiological classification of soil bacteria based on their energy and carbon sources.

Energy source	C source	Classification
Light	CO_2	Photoautotrophic or photolithotrophic
Light	Organic C	Photoheterotrophic or photoorganotrophic
Chemical	CO_2	Chemoautotrophic or chemolithotrophic
Chemical	Organic C	Chemoheterotrophic or chemooorganotrophic

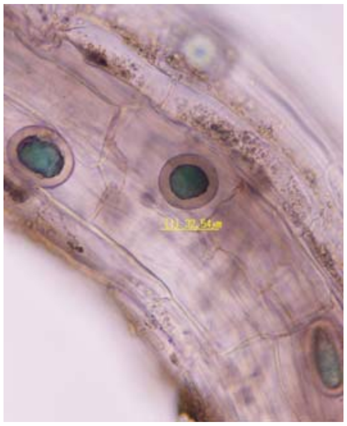

Figure 5: Spores of non-mycorrhizal fungal endophyte in the root of forage grass. Little is known on root-inhabiting non-mycorrhizal fungi, sometimes referred to as dark septate endophytes. Their growth form outside the roots has not yet been described.

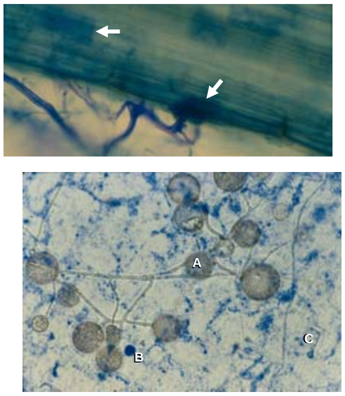

Figure 6: Top: point of entry of an AM fungi in a root of alfalfa. Arrows indicate fungal growth in the root. Bottom: (A) extraradical mycelium with spores of the fungus, beside (B) the spore of a fungal pathogen (*Phytophtora megasperma*), and (C) a nematode.

In soil, AM fungi form dynamic hyphal networks, which are shared by plants. These hyphae can form anastomosis, i.e., can fuse to form connections through which cytoplasm and nuclei can flow. In undisturbed soil, these AM hyphal networks appear to be permanent, but they are actually dynamic structures with hyphal life spans of about 5 days. As older parts of mycelia senesce, growth proceeds from hyphae tips and the cytoplasm is carried forward[13]. In several AM fungal taxa, anastomosis may reconnect different parts of a mycelium that were broken as a result of senescing hyphae or grazing by the soil fauna.

The term "rhizobia" strictly refers to members of the genus *Rhizobium*, but it is usually used to refer to all bacteria capable of nodulating legumes and fixing nitrogen in the nodules that they form. As more legume species are studied, and molecular methods used to characterize rhizobia, the taxonomy of rhizobia changes. The latest count has seven genera and 48 species[30]. The seven genera are: *Rhizobium, Bradyrhizobium, Sinorhizobium, Azorhizobium, Mesorhizobium, Allorhizobium* and *Agrobacterium*.

Fig. 7. Left: rhizobia cells colonizing a legume root. Right: Nodules that result from successful infection of legume roots by rhizobia. Pink nodule interiors (from leghaemoglobin) indicate that nitrogen fixation is occurring.

Functions and Interactions

Soil fauna

Bacteria and fungi are the primary agents responsible for soil organic matter decomposition and nutrient cycling. However, soil fauna, through their interaction with microflora, also exert substantial indirect influence. The feeding activity of soil fauna leads to fragmentation and partial digestion of plant material that allows for more accelerated subsequent microbial decomposition. The movement of fauna through soil increases dispersal of microbial reproductive structures if they become attached to faunal bodies or enter the gut and are deposited in fecal material. The burrowing activity of earthworms enhances soil fertility and soil structure by mixing organic material with subsurface soil. Soil material excreted by earthworms (earthworm cast) is high in plant available nutrients and improves soil structure. Earthworm tunnels create a pore system that enhances soil aeration and water infiltration. Further, the walls of earthworm burrows are lined with mucous excreted by the earthworms and are hotspots of microbial activity and associated plant nutrient release.

Soil microorganisms

Soil organisms are very important in agriculture because they mediate many beneficial processes that include:

(a) Recycling of plant nutrients: Nutrients like nitrogen, phosphorus and sulphur occur mostly as organic compounds (in manures, compost, crop residues, soil organic matter etc) that are not available for plant uptake. During decomposition, soil microorganisms break these compounds and convert the nutrients into inorganic forms that plants can uptake through their root systems. Meeting some crop nutrient requirements through recycling reduces the need for fertilizer.

(b) Nitrogen fixation: Plants (or animals including humans) cannot directly utilize the abundant nitrogen present in the air we breathe. In the nodules of leguminous plants, soil microorganisms called rhizobia convert (fix) gaseous nitrogen to a form that plants (and animals feeding on plants) can utilize. Because legumes meet most of their N requirements from nitrogen fixation, they usually don't require inorganic nitrogen fertilizer. Non-legume crops grown in association or in rotation with legume crops usually have reduced fertilizer N requirements. Therefore, nitrogen fixation has both economic and environmental benefits. There exists "free-living" and "rhizospheric" bacteria in the soil capable of fixing atmospheric nitrogen. However, the amounts fixed are small in comparison to symbiotically-fixed nitrogen occurring in legume root nodules.

(c) Maintenance of soil structure: Good soil tilth results from aggregation of soil particles, held together by fungal hyphae that act as sticky strings, and microbial excretions that act like glue. Soils with good tilth are less susceptible to erosion, have better water infiltration and aeration, and offer less resistance to plant germination and root penetration, than soils with inferior soil tilth.

(d) Degradation of agrochemicals and pollutants: Many pesticides that are applied to soil or fall on the soil would have serious residual effects if they were not degraded by soil microorganisms. Un-degraded agrochemicals would also contaminate water supplies. Soil pollutants like polychlorinated biphenyls (PCBs) have successfully been degraded by soil microorganisms.

(e) Biological pest control: Soils with active microbial communities have fewer pest problems because of biological control through predation, antibiotic production and competition for resources. Given biological pest control, pesticide use can be reduced.

Therefore, soil management systems that foster the development of healthy, diverse microbial communities are usually more sustainable than those that do not.

Germinating plants soon become connected to common AM fungal networks in soil. AM fungi hyphal networks mobilize soil nutrients. These hyphae explore the soil beyond the reach of plant roots. Nutrients are loaded in the hyphae, rapidly transported within AM fungal networks, and downloaded into the plant symplast. This rapid transport is particularly important for nutrients like phosphorus, copper and zinc, which do not move with water toward plant roots as plants absorb water. AM fungi are also known to protect plants against soil-borne pathogens. Protection is provided through improved nutrition, but also through soil sanitization[17]. Their presence in soil can reduce the number of propagules of important pathogens such as *Fusarium* and *Pythium* species.

DSE have diverse ecological roles, and this is no surprise considering the heterogeneity of the group. Many are involved in stress reduction in plants. They may be important for plants to access nutrients from organic pools, for improved plant tolerance to pathogen attack, drought, heat, and grazing stresses, and may influence plant community dynamics[23].

Impact on Soil Properties

Soil fauna

The most important influence of microfauna on soil properties is probably their ability to modify microbial processes. Selective grazing of fauna on bacteria and fungi influences microbial community composition and function and the rate and nature of organic matter decomposition and nutrient cycling. Larger fauna, when present, may have a more significant physical impact on soil properties. The consumption of plant residues combined with their burrowing activity mixes organic matter with soil to enhance soil fertility and soil structure. Additionally, their tunneling activity improves gas exchange, water infiltration and root proliferation.

Soil microorganisms

Soil microorganisms are bio-indicators of soil health. Soil health is the continued capacity of the soil to function as a vital living system, within confines of its ecosystem and land-use, to sustain biological productivity, promote air and water quality, and maintain plant, animal and human health[8]. Soil health embodies the idea of soil as a living system which contains many organisms that perform various functions critical to agriculture and to life on earth in general. Soil microorganisms are good bio-indicators because they are sensitive to soil management and climate change.

AM fungi increase carbon input in soil by increasing plant productivity; they rely on plant photosynthesis for their own carbon requirements. About 4-20% of the total carbon photosynthesized by plants is used by AM fungi for their metabolism[27]. This represents an important input of carbon to the soil. The cell wall of AM fungi contains chitin, a resistant compound to microbial breakdown. Therefore, the carbon in AM fungal residues remains in the soil for a relatively long time. AM fungi improve soil structure through their extensive hyphal networks by acting as sticky strings that hold and package soil particles and microaggregates into macroaggregates. Carbon input to soil and improvement of soil structure with hyphal structures may partly explain the influence of AM fungi on the soil microbial community. AM fungi associations with roots also stimulate decomposing microorganisms that release nitrogen to the host plant[2].

If a legume crop is grown in the same soil for a long time, the population of indigenous rhizobia increases. In ancient times, portions of such soils were excavated and used to inoculate legumes in a different field. This practice is not necessary today, given the availability of efficient strains in rhizobial inoculants.

Distribution of Soil Fauna and Microflora in Prairie Soils

Soil fauna

In a 1967 International Biological Program study, soil fauna were counted in the semiarid grassland of southwestern Saskatchewan[25, 29]. The populations (Table 2) were low compared to studies from more favorable climates. Interestingly, no earthworms were identified in this study. The last glacial period in the prehistory of Western Canada is thought to have destroyed indigenous earthworms. They were apparently re-introduced to cultivated soils by pioneers who settled in Canada from various parts of Europe. Recent studies report higher earthworm populations in no-till than in conventionally tilled fields[5] (Table 1).

Table 1. Populations of various soil organisms in the top 30 cm of soil at two Western Canadian sites[5, 25, 29].

Location	Faunal group	Sampling time	Average population
Matador, SK, grassland	Nematode	1968 to 1971	8,510 per m^2
Matador, SK, grassland	Arthropod	1968 to 1971	106 per m^2
Matador, SK, grassland	Annelid (enchytraeid)	1968 to 1971	30 per m^2
Matador, SK, grassland	Bacteria and Actinomycetes	1968 to 1970	1.2 million per g soil
Lethbridge, Alta., zero tillage	Annelid (earthworm)	Aug 1992 & May 1994	183 per m^2
Lethbridge, Alta. Conventional tillage	Annelid (earthworm)	Aug 1992 & May 1994	3 per m^2

Soil microorganisms

Because most soil microorganisms depend on organic carbon for energy and growth, their distribution in arable prairie soils will depend on their organic carbon contents. Thus, a Black Chernozem usually harbours more soil microorganisms than a Gray Luvisol soil. The climate of the region is also an important factor, e.g., cold vs. warm soils, dry vs. moist soils, etc. In agricultural soils, different soil management practices also impact on soil microorganisms.

AM hyphae are abundant in the top 20 cm of soil, where they can account for up to 25% of total soil microbial biomass. One gram of top soil can contain 100 metres of AM hyphae[16]. But differences in abundance and diversity of AM fungal species according to soil type have been observed. They are more abundant and diverse in Dark Brown Chernozems and Grey Luvisols than in the dryer Brown soils, and were rare in Vertisols, which are characterized by high clay content. Cropped prairie fields appear to host less than half the level of AM fungal diversity found in the soil of Grasslands National Park, indicating a negative impact of cultivation on AM fungi. DSE are most often encountered in extreme environments, supporting their role in plant drought stress mitigation, and are prolific in the roots of prairie grasses, where they can outnumber AM fungi[14].

The presence of indigenous rhizobia in the soil is dependent on the history of legume crops. For example, populations of pea-nodulating rhizobia in Alberta were 1-100 rhizobia/g in wheat fields that had never had legumes grown in them, but populations in fields planted to peas were 100-1,000 times greater[15]. Another important factor is soil acidity; acid soils usually contain less rhizobia than near-neutral soils. Rhizobial population numbers are important. In soils with indigenous rhizobial populations greater than 1,000 rhizobia/g soil, response to inoculation with commercial inoculants is often limited. Indigenous rhizobia out-compete inoculant rhizobia in forming nodules, and indigenous rhizobia are usually less effective at nitrogen fixation than the carefully-selected strains contained in commercial inoculants.

Soil Management Effects

Tillage

Soil fauna

In general, soil management systems that include some form of conservation tillage combined with soil water conservation promote the development of soil faunal populations. Tillage has a more deleterious affect on macrofauna than microfauna.

Soil microorganisms

Soil microbial biomass, populations and diversity are usually greater under no-till than conventional-till[3, 18, 22]. These differences are often observed only in the top few centimetres of soil because crop residues are left on the soil surface under no-till. These residues increase organic carbon in the top soil, and most soil microorganisms depend on organic carbon for energy and growth. Under conventional tillage, soil organic carbon decreases due to more microbial breakdown and soil erosion than under no-till. Soil disturbance under conventional-till can also reduce microbial populations because of more rapid drying of the soil, mechanical destruction of soil aggregates, soil compaction and disruption of access to food resources. Furthermore, rotating crops under no-till means that litter accumulated from different crops in preceding years offers a greater variety of food or carbon sources to soil microorganisms than in tilled soils where litter does not accumulate.

Soil microbial activity, expressed as CO_2 (carbon dioxide) evolution in the field, is usually reduced more under no-till than conventional-till[7, 22]. Greater microbial breakdown of organic carbon under conventional tillage results in greater CO_2 evolution. Therefore, a no-till system will potentially sequester more soil carbon and contributes less microbial CO_2 to the atmosphere than conventional tillage.

Tillage fragments AM hyphal networks in soil. But AM mycelia are distributed throughout the top 20-25 cm layer of soil and since tillage is usually shallow (about 7 cm deep), it is assumed that tilling prairie soils has limited impact.

Crop rotation

Crop rotation usually increases soil microbial diversity by providing more diverse substrates of crop residues to soil microorganisms. Legume-based crop rotations usually have greater microbial populations, biomass, diversity and activity than cereal mono-cropping rotations[21, 22]. The keyword is "rotation" because legume monocropping is not good either. For example, in Saskatchewan, the soil in continuous pea cropping had a smaller soil microbial community and less beneficial bacteria and mycorrhizal fungi than the soil in a wheat-pea rotation[24].

AM fungi are obligate biotrophs, i.e., they are unable to complete their life cycle without a host plant. This biotrophy may explain the negative impact of summer fallow[1] and canola[11] (a non-host crop) on mycorrhizal development in subsequent crops. Summer fallowing is still somewhat common in the Brown soil zone and this may explain the lower abundance of AM fungi in these soils. Canola-wheat rotations are common in the Black soil zone and they may be responsible for the low abundance of AM fungi in these soils. As noted above, soils in rotations that host legume crops with specific rhizobia will have higher populations of those rhizobia than soils in rotations without host legumes.

Inorganic fertilizers

Soil fauna

Fertilizer application, when accompanied by increased plant growth, usually increases faunal growth. The influence of agricultural lime used to reduce soil acidity is variable, with some European studies reporting an increase in earthworm populations and others decreased enchytraeid populations and activity[26].

Soil microorganisms

Fertilizers can have positive or negative effects on soil microbial communities, and these effects can be direct or indirect. One direct, positive effect is increase in microbial growth because fertilizers contain nutrients for microbial metabolism. A related but indirect effect is that fertilizers increase crop growth which in turn increase root exudation during crop growth and makes more crop residues available after harvest. Root exudates and crop residues contain organic carbon substrates for microbial metabolism. Negative direct effects of commercial fertilizers on soil microbial communities include toxicity in the injection zone, especially with anhydrous ammonia. One indirect negative effect is the soil acidifying nature of some inorganic fertilizers containing nitrogen (e.g., urea and anhydrous ammonia) or sulphur (ammonium sulphate). Prairie soils tend to be alkaline; they buffer fertilizer acidifying effects.

Fertilizers applied at recommended rates for crop production do not usually affect soil microorganisms and generally have positive effects. However, accumulation of residual phosphorus fertilizer in soil can repress AM fungal proliferation and symbiotic formation in plant roots. In addition, application of nitrogen fertilizer can reduce nitrogen fixation. The legume plant uses a lot of energy to fix nitrogen. If the legume is grown in soil with high levels of inorganic nitrogen, soil N will preferentially be used. The plant will reduce or shut down nodulation and/or nitrogen fixation. "Starter nitrogen" applications < 30 kg/ha may be beneficial to the plant in N-deficient soils because the nitrogen fixation process takes weeks to get established, but higher amounts tend to be wasteful because they reduce nitrogen fixation.

Organic soil amendments

Organic inputs (manures, composts, crop residues, etc.) are added to soil to provide nutrients for crop growth and organic carbon for soil microbial growth as well. Some of these amendments also contain microorganisms. The diverse and vibrant microbial communities induced by organic soil amendments play a role in suppressing soil-borne plant pathogens. However, high rates of manure applications increase the risk of introducing nutrients and pathogens in water systems. Organic amendments usually increase AM development. Several compounds from decomposing organic matter have been found to stimulate AM fungi[12].

Pesticides

Soil fauna

Herbicide use is generally not injurious to soil fauna unless the herbicide removes a food source and indirectly contributes to a population decline. Insecticide application is generally deleterious to faunal populations, but the populations usually recover.

Soil microorganisms

Herbicides applied at recommended rates usually have no adverse effects on soil microbial biomass or diversity[4, 20]. However, shifts in the composition of microbial communities have been observed[19, 20]. Such shifts can lead to successions in microbial communities that could have long-term effects on soil biological processes. In a study of seed-applied fungicides, Thiram® and Captan® reduced populations of rhizobia on the seed, but only the highest fungicide concentrations reduced pea nodulation and growth[10].

Genetically-modified crops

Genetically-modified crops can affect soil microorganisms due to differences in the amount and composition of root exudates, gene transfer from the transgenic crop, and effects of management practices for transgenic crops, e.g., pesticide applications. Differences in amounts and composition of decomposing crop residues can also affect soil microorganisms. In Saskatchewan, shifts in bacterial community composition in the rhizosphere of herbicide-resistant canola varieties were observed, but the changes did not persist into the following growing season[9]. Differences in endophytic bacterial communities were also observed in these studies, but their implications are not clear.

Concluding Remarks

Soil organisms are important in agriculture because they mediate many useful biological processes like nutrient cycling and biological pest control. These processes should be encouraged by adopting soil and crop management practices that foster the development of healthy, diverse communities of soil organisms. Such practices include no-till, diversified crop rotations, proper fertility management and the application of organic manures, when possible.

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