

Symbiotic Root Fungi

Chantal Hamel, Juan Carlos Perez, Tandra Fraser and Atul Nayyar
Semiarid Prairie Agricultural Research Centre (SPARC), AAFC

Soil biodiversity and microbial resources

The soil is highly favourable to life, which proliferates abundantly in its environment. In soil, life mostly occurs in the form of numerous minute organisms embedded in the soil matrix and invisible to the naked eye. At the microbial scale, the soil matrix is highly heterogeneous, a condition favouring the emergence of biodiversity. By far, most of the biological diversity of the Earth is contained in soil. Soil biodiversity is tremendous with 5000-10000 species of microorganisms per gram (Wardle et al. 2004). This biodiversity is both a precious resource and a complication. A world of interactions is intertwined in this biodiversity. These interactions are dynamic and influenced by soil physico-chemical conditions, which vary with the weather, seasons, and cropping systems. The vast majority of soil microorganisms are non-culturable, adding to the difficulty of studying soil taxonomic and functional diversity. We know very little about soil bioresources and functioning, but contemplate the astonishing complexity of the living soil.

Soil microorganisms are a component of soil quality. They are involved in soil fertility processes and in the maintenance of soil structure stability. Some promote plant growth, while others cause plant diseases. Thus, the management of soil microbial resources is important. In crop production, soil microbial resources are managed through strategies developed for the preservation or improvement of soil quality. Well planned crop rotations effectively break disease cycles and promote crop health, and nitrogen fixing bacteria are successfully inoculated in legume crops. But beyond this, the management of soil microbial resources has been very limited and largely restricted to the biocontrol of pests in greenhouse production. The complexity of the soil systems makes the management of soil microorganisms in the field difficult and the results of interventions have often been highly unpredictable (Savka et al. 2002).

Research efforts toward the management of soil microbial resources have been concentrated on key functional organisms such as biocontrol agents and plant symbiotic organisms. The interest in plant symbionts comes from the fact that they often enhance plant growth. We also believe that it might be easier to manipulate plant-associated microorganisms than free-living microorganisms, since we know how to manipulate plants they depend on. Arbuscular mycorrhizal fungi (AMF) are plant associates involved in plant nutrition, biocontrol, and soil structure stabilization. They have been intensively studied and are relatively well understood. Other fungi, called dark septate endophytes (DSE) are less well known but have often been reported to exist in the plant roots. AMF and DSE are symbiotic root fungi with potential positive effects on agricultural productivity. Details of these fungi and on their impact on plant growth are summarized in this text.

The root symbiont lifestyle

Symbioses are widespread in the living world. Microorganisms sheltered in the rumen contribute to the digestion of complex carbohydrates and improve the nutrition of ruminants. Bees pollinate the flowers feeding them enhancing seed set and reproduction in numerous plant species. Symbioses are adaptations through which different organisms team up and share their capacity and strengths. Symbioses involving plants are common and diverse. In symbiotic plants are usually providers of C and energy, two precious trading products that often limit biological activity. Plants can utilise solar energy and atmospheric C (CO₂). These resources are abundant but can only be accessed through photosynthesis. Fungi can acquire these resources indirectly via an association with photosynthetic organisms like plants. Whereas pathogenic fungi often destroy plants while acquiring the C and energy stored in their tissues, symbiotic organisms utilise a more effective strategy. They generally enhance plant health and productivity, thus, improving their C and energy source. The symbiotic way of life is highly effective and through evolution it has become the norm rather than the exception in the Plant Kingdom.

Mycorrhizal fungi

Plant roots are almost always involved in some kind of symbiosis with mycorrhizal fungi. These fungi are typically effective in the capture of soil-derived nutrients and enhance their host plant productivity largely by feeding them. They provide their host with mineral nutrients of low availability to plants such as P, a nutrient with low solubility in soil, and organic forms of N, which require mineralization prior to plant uptake.

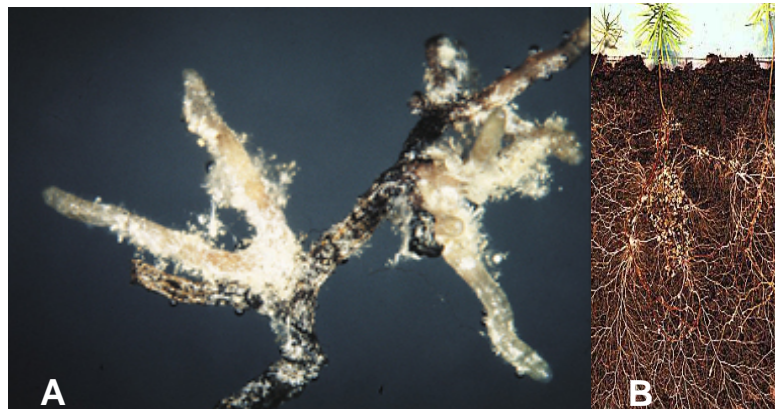


Fig. 1. (A) The ectomycorrhizal fungi *Tricholoma magnivelare* on *Pinus contorta* (from Michel LefèvreI) (B) Ectomycorrhizae established in an observation box.

Mycorrhizal symbioses are classified based on morphological features such as the extent of fungal partner penetration into host plant tissues and fungal coverage of the host root (Smith and Reid 1997). Ectomycorrhizal fungi typically form a sheath on the root surface (Fig. 1) and their growth in host roots is intercellular. These fungi are associated with several tree species in forest systems under temperate climates where organic matter accumulates into an organic horizon overlaying the mineral soil. Ectomycorrhizal fungi enhance their host plants N and P nutrition through mineralization of soil organic matter and by extending the absorptive surface available for plant uptake. They also reduce disease incidence and enhance the solubilization of minerals (Hoffland et al. 2004).

Endomycorrhizal fungi do not form a sheath on roots but penetrate their host plant cell wall. Endomycorrhizal associations are diverse. Some are specific and restricted to certain groups of plants. Orchids form orchidoid mycorrhizae and species of the Ericaceae form ericoid mycorrhizae. Fungi involved in orchidoid associations provide C to orchid embryos compensating for the lack of reserve material in orchid seeds. The cortex of ericaceous plants is made of a single layer of cells intensively colonized. Fungi involved in ericoid associations provide their host with both P and N. Nutrient availability in soil where ericaceae species proliferate is reduced by low pH conditions inhibiting mineralization of organic residues; mycorrhizal fungi allow ericaceae to exploit soil organic matter. The most widespread type of endomycorrhizal symbiosis is largely unspecific. It forms between the majority of land plant species and fungi of the Glomeromycota, a phylum of the Kingdom Fungi, commonly called arbuscular mycorrhizal fungi (AMF). AMF are involved in symbiosis with crop plants and thus, is the group of mycorrhizal fungi that has raised most research interest. They are described in greater detail in the following two sections.

Form and functions of arbuscular mycorrhizal fungi

AMF are abundant in soil. They account for about 25% of agricultural soils' microbial biomass (Hamel et al. 1991; Olsson et al. 1999) and live in symbiosis with about 80% of land plant species, including the most economically important ones¹. The arbuscular mycorrhizal association was so successful that in the course of evolution, AMF became obligate biotrophs i.e., they can not live without connection to, and carbon supply from, a living host plant. This feature has important implications on the life of AMF in cultivated soils. AMF are found close to plant roots and most of their biomass is in the top 0-20 cm of the soil (Kabir et al. 1998b). They are most abundant directly under the row, thinning out in between the rows of row crops such as maize (Kabir et al. 1998a). Bare fallow periods reduce the vigour of their population (Kabir et al. 1999).

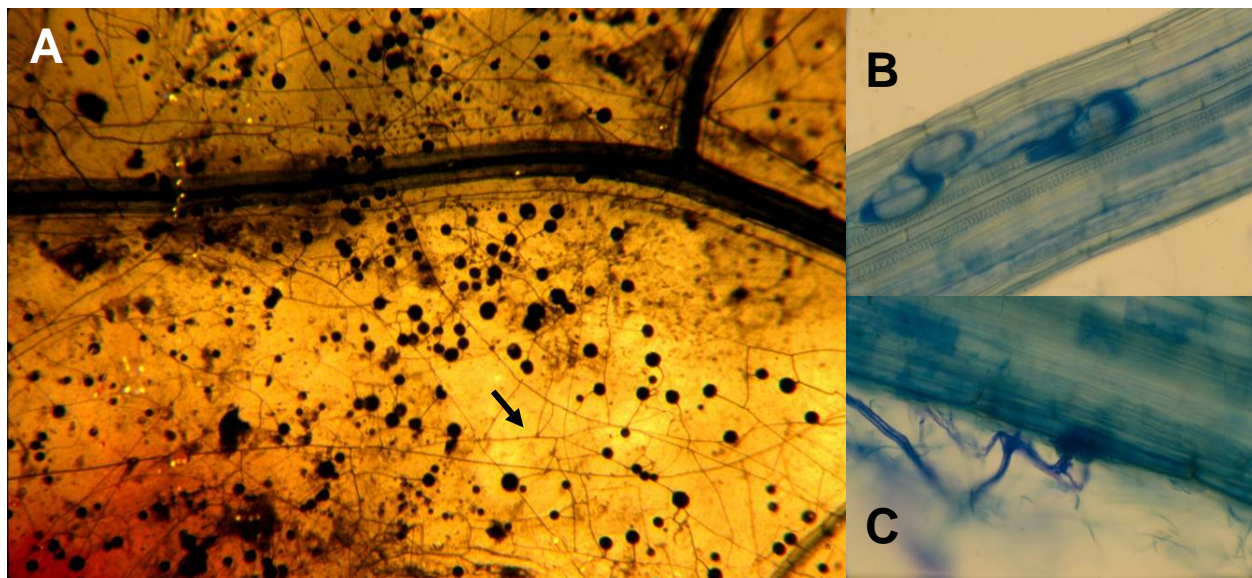


Fig. 2. *Glomus intraradices*, an arbuscular mycorrhizal fungus. (A) Extraradical hyphal network associated with alfalfa roots growing in soil. The arrow indicates a point of anastomosis. (B) Vesicles and hyphal colonization and (C) hyphal penetration point in carrot roots (courtesy of Line Nantais).

Physically, AMF appear as networks of fine tubes of a few micrometers in diameter, filled with cytoplasm, and producing spores (Fig. 2). These networks are extensive, often with tens of meters per gram of soil (Leake et al. 2004). It is important to keep in mind that AMF isolates are not all the same, and vary functionally and morphologically. Isolates capable of anastomosis can theoretically grow hyphal networks as large as four 1-mile² section i.e., from road to road, while the isolates unable to fuse may be seen as hair-like structures on roots. These networks, enmeshing the soil matrix, connect to plant roots, spreading internally, and penetrating cell walls of the root cortex area without disrupting plant cells' plasma membrane, where they acquire carbon- and energy-rich photosynthesis products (Hamel 2007). In turn, plants tap in on the mineral nutrients contained in these networks. AMF networks were shown to provide plants with all essential nutrients, but they are particularly important as a source of P, Cu and Zn (Liu et al. 2007). These nutrients have low solubility in soil and are often found in low concentrations in the soil solution. Thus, they are more difficult to extract from the soil matrix than highly soluble nutrients such as nitrate-N, for example.

AMF are useful to insure the adequate nutrition of their host plant, but they also are a very important component of soil quality (Jeffries et al. 2003; Six et al. 2004). Their 'sticky' hyphae and soil enmeshing hyphal networks contribute importantly to soil aggregate stabilization (Six et al. 2004), enhancing soil aeration and water infiltration, and reducing the erodibility of soils. AMF's abundant mycelium, which is supplied by plant photosynthesis, distributes carbon compounds in soil. Carbon availability is the factor generally limiting the activity of soil microorganisms. Carbon distribution in soil may be the major mechanism explaining the relationship between AMF and soil microbial diversity, and the impact of these fungi on the structure of soil microbial communities (Andrade et al. 1998; Marschner and Baumann 2003). Soils abundant in AMF are healthier and have been associated with reduced population of soil-borne pathogens and disease incidence (Dehne 1982; St-Arnaud et al. 1995).

Factors affecting arbuscular mycorrhizal fungi

In their quality as a product of 400 million years of co-evolution with plants and soils (Pyrozinsky and Dalpé 1992; Redecker 2002), AMF play a key role in the balance of the soil ecosystem. It might be wise to preserve these fungi in agricultural soils. Arbuscular mycorrhizal associations differ from pathogenic associations in that plants control the growth of their associated AMF. This regulation is based on nutrient availability to plants (Liu et al. 2007). When availability is low, the level of mycorrhizal colonization increases, presumably along with carbon input to AMF; when availability is high, plant investment in AMF network development decreases. Since AMF have mineral nutrients requirement of their own, increasing nutrient availability may increase AMF network growth (Balsler et al. 2005) up to a level beyond which reduced plant carbon supply becomes limiting.

Low soil pH (Hamel et al. 2005), prolonged periods of time in absence of host roots during a fallow (Kabir et al. 1997), or a non-host phase of a crop rotation (Fraser et al. 2006) are factors adversely affecting AMF development. A high population of AMF predators, such as fungi feeding nematodes or springtails, in the soil environment may result in yield losses by transforming AMF into an important carbon drain to plants (Giannakis and Sanders 1990).

Dark septate fungal endophytes

A large number of other apparently non-pathogenic and non-mycorrhizal fungi were sometimes observed in the roots of plants known to form arbuscular, ericoid, orchidoid and ectomycorrhizae, as well as in the roots of non-mycorrhizal plants (Jumpponen and Trappe 1998).

These fungi have been commonly referred to as “dark septate endophytes” (DSE). The DSE appellation is a mixed bag from which no general pattern has emerged regarding the specificity or function of the fungi involved. DSE is an heterogeneous group of endophytic fungi, which are not all dark, in spite of their appellation. DSE were associated with plant growth stimulation (Varma 1999; Waller et al. 2005), resistance to extremely high temperature (Redman et al. 2002), and early season nitrogen uptake (Scharndl et al. 2004). Barrow (2003) proposed that some DSE systematically colonizing rangeland plants maintain the hydraulic continuity between plants and dry soil, enhancing nutrient and water uptake in chronically dry ecosystems, and protect roots against excessive desiccation during drought periods. This effect may be attributable to the creation of a protective zone in the rhizosphere through abundant lipid production by these DSE.

As reported by Barrow (2003), we found that the abundance of DSE in the roots of rangeland grass species may exceed that of AMF. We found over 30% of root colonization by DSE in healthy native and tame forage plant species growing in semiarid Saskatchewan. In the top 0-15 cm layer of the soil, root colonization was shared by DSE and AMF mycelia, but in deeper layers, roots were colonized almost exclusively by DSE. In a controlled condition experiment, DSE isolated from crested wheatgrass and Russian wild rye preferentially colonized the roots of the plants species they were originally associated with, indicating that these DSE are host specific. Obviously, more research is required to understand the role of DSE on plant growth under arid conditions. Such research may lead to the development of methods to enhance the sustainability of our agricultural industry and mitigate the impact of global change on Canadian agriculture.

Conclusion

Symbiotic root fungi are soil resources with high potential for application in agriculture. They are an important component of soil quality through their involvement in plant growth promotion and protection, and in soil structure stabilization. Because of their close relationship with plants, they should be more manageable and reliable than free-living microorganisms, which depend on unpredictable and often unknown soil factors. The management of soil microbial resources appears as an essential strategy in a sustainable world. Degradation of environmental quality in some intensively managed areas indicates a need for human interventions more harmonious with

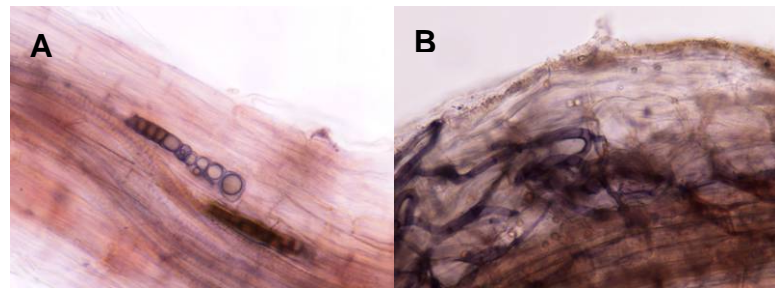


Fig. 3. Dark septate endophytes in the roots of crested wheatgrass. (A) Spores associated with hyaline hyphae; (B) dark septate mycelium.

nature. Such practices will be based on improved understanding of the natural systems and, in particular, the living soil.

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