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Review

Root-soil physical and biotic interactions with a focus on tree root systems: A review

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ABSTRACT

Our perception of plants is determined by their visible organs: stem, branches and leaves. The underground parts of a plant are rarely seen; indeed the root system is usually hidden from sight. This is also reflected in science where the interaction between leaves and the atmosphere is much more studied than interactions between roots and soil. One reason for such an imbalance involves the difficulties in studying roots in their heterogeneous and opaque environment. Consequently, relatively little is known about the importance of roots in the soil and how soil physico-chemical properties and soil organisms are influenced by the presence of roots and vice versa. Roots are not merely a passive agent that grow in a challenging environment: roots are engaged in a tremendous number of interactions with soil, which change soil properties and enhance its biotic component.

This paper reviews the current state of understanding on the factors involved in root-soil interactions, bearing in mind the specific aim of underlining more recent advances to identify significant gaps in this research field. We also promote a tree-oriented view of roots, describing how soil physico-chemical properties, micro- and macro-fauna, symbiosis and pathogens affect tree root growth and how roots can interact and modify these abiotic and biotic factors.

We hope our review will provide an impetus for more studies on the intricate soil-root interactions to enhance the importance of this vast, and somewhat hidden topic.

1. Introduction

Plants grow at the interface between soil and the atmosphere making their way into both. Soils are the biologically active part of the outermost layer of the Earth's crust that ranges in thickness from a few centimetres to several decimetres. Soils can be covered by vegetation and penetrated by roots (Blume et al., 2015). There are different soil types and each presents typical physical properties depending on structure, particle distribution, pore size distribution, water and air storage capacity and biotic composition (Blume et al., 2015). Roots are commonly defined as the vegetative organ that anchors the plant to the soil, takes up water and nutrients and stores non-structural carbohydrates for later use (Evert, 2006). Despite their commonly known functions, root systems can reveal a fascinating complexity (Hodge et al., 2009).

The huge variety of root structures found in plants is the result of a combination of plant root-soil interactions that have evolved over time. The first vascular plants (Rhyniophyta) lacked roots; in fact roots evolved in the seed plant clade, as well as lycophytes, sphenophytes and ferns, in response to selective pressure from the land environment and increasing plant size (Beck, 2010). However, root morphology has changed relatively little over time since protected subterranean environments prevent the intense and variable selection pressures that stems endure. Nevertheless the root system is still a highly diverse and specialized organ, both morphologically and ecologically (Ingrouille and Eddie, 2006). These same root-soil interactions are currently guiding root development in extant plants.

Observational techniques for analysis of root system architecture of woody species and their interactions with soil have been limited mainly due to difficulties in accessing intact root systems (Reubens et al., 2007; de Dorlodot et al., 2007; Lynch, 2007). Roots are hardly visible and difficult to sample (Gyssels and Poesen, 2003; Jansen and Coelho Netto, 1999; Waisel et al., 2002), moreover many of the known investigation methods are time-consuming and damage the root system to be studied (Böhm, 1979; Kaspar and Bland, 1992; Maeght et al., 2013). These methodological problems are very pronounced when studying shrubs and trees that don't grow under controlled soil conditions and are surrounded by large and unequally distributed root systems of

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neighbouring plants (Reubens et al., 2007). Different root systems measurement methods are applied depending on the functions to be investigated (i.e. anchorage, absorption of nutrients and water, or symbiosis) (Danjon et al., 2013).

Despite advances in root studies in recent decades, the method used most frequently to obtain information about tree root architecture is still excavation (Weaver, 1919; Stoeckeler and Kluender, 1938; Mitchell and Black, 1968; Newton and Zedaker, 1981; Rizzo and Gross, 2000). This is a destructive and very labour intensive method that allows the uprooted coarse root systems to be mapped layer by layer (Maeght et al., 2013). Furthermore, with this technique, the coarse root system can be digitized to provide detailed, reliable and valuable results (Danjon et al., 1999a,b; Oppelt et al., 2001; Dupuy et al., 2005; Wagner et al., 2010, 2011). Less destructive methods that produce vertical information (i.e. 2D) are coring (Böhm, 1979; Cahoon et al., 1996) and (mini)rhizotron (Kage et al., 2000; Hummel et al., 1989; Liedgens and Richner, 2001; Taylor et al., 1990; Gijsman et al., 1991; Vercambre et al., 2003) techniques. Non-destructive imaging techniques of root system architecture are X-ray computed tomography (Pierret et al., 1999; Brown et al., 1991; Lontoc-Roy et al., 2004), and ground-penetrating radar (GPR) (Wielopolski et al., 2002; Butnor et al., 2001) used and tested in forest, woodland and urban environments (Hruska et al., 1999; Sustek et al., 1999; Stokes et al., 2002). The GPR technique is not efficient in detecting roots in the vertical plane as the radar signal cannot identify objects running parallel to the transmitted electromagnetic waves (Stokes et al., 2002). Advances in the software are necessary in order to process root architecture data faster and more accurately (Stokes et al., 2002). Studying and improving these techniques can have important consequences not just for the measurement and analysis of woody root architecture but also for the understanding of physical and biotic soil-root interactions.

This paper reviews how soil physico-chemical properties affect tree roots architecture, while also taking into account the active role of plant roots in modifying soil properties as well as the interactions between roots and biotic forms living in the soil. We describe how soil physico-chemical properties, micro- and macro-fauna, symbiosis and pathogens affect tree root growth. The focus is on trees as the available knowledge on tree roots is relatively scarce.

2. Abiotic factors and tree roots

Soil structure is made up of micro and macroaggregates containing solid (mineral particles), liquid (mainly water) and gaseous (air) phases as well as soil organisms (Blume et al., 2015; Lavelle et al., 2001; Gregory, 2008). Plant roots play a major role in the formation of aggregates (Hunt and Coleman, 1987; Paul and Clark, 1998; Griffiths, 1965; Cheshire et al., 1984; Puga-Freitas and Blouin, 2015). During growth, roots compress the surrounding soil thereby facilitating the formation of new, small aggregates (Dexter, 1991) while absorbing water and causing the surrounding soil to shrink.

The influence of plant root growth on physico-chemical soil properties has been studied almost entirely on young crop root systems in controlled growing conditions (Gregory, 2008). Such closed systems allow both better environmental control and easy access to roots for measurements, but may not reflect the behaviour of older root systems that have acclimated to their particular soil environment (Gregory, 2008). Literature on woody shrubs and trees related to these topics is still largely lacking (Espeleta et al., 1999; Fernández et al., 1991). In this section we will see how soil properties influence root growth and how root systems influence soil properties (Jones et al., 1997, 2006, 2009).

2.1. Soil temperature

It has been demonstrated that soil temperature affects growth on root system components, initiation and branching, orientation and direction of growth and also root turnover (Kaspar and Bland, 1992; Cooper, 1973; Eissenstat and Yanai, 2002). The minimum and optimal soil temperatures for root growth and respiration are typically within the ranges of 0–12 °C and 25–35 °C, respectively, while the maximum is typically 40–45 °C (Gregory, 2008), depending on the plant species and origin (McMichael and Burke, 1996; Kramer and Boyer, 1995; Bouma et al., 1997). In 1995, Lyr and Garbe studied the specific optimum temperature for *Tilia cordata* (20 °C), *Fagus sylvatica* (20 °C) and *Quercus robur* (25 °C), while Seiler (1998) studied it for *Helianthus sp.* (25–30 °C). If the temperature of the soil differs significantly from the species-specific optimum then the structure and function of the root system can be altered (Faget et al., 2013).

With temperatures lower than the species-specific optimum; root hydraulic conductivity decreases and slows the meristematic activity of root tips (Aroca et al., 2001, 2005; Melkonian et al., 2004). The most common morphological responses are plants producing smaller and less branched root systems with roots of thinner diameters (Brouwer, 1964; Pahlavanian and Silk, 1988; Nagel et al., 2009).

With extremely high temperatures, plants adopt different techniques to reduce the release of carbon and water by roots. Many grass species and desert succulents shed fine lateral roots (Eissenstat and Yanai, 1997; Huang and Nobel, 1993), *Citrus* greatly reduce respiration (Kosola and Eissenstat, 1994; Bryla et al., 1997; Espeleta and Eissenstat, 1998), whereas cotton (Arndt, 1937) and maize (Fortin and Poff, 1991) decrease root elongation rates. The different behaviours can be attributed to varying root types. Species with coarse roots and a heavily lignified exodermis will tend to tolerate dry soils, reducing carbon losses by minimizing respiration in times of drought (Eissenstat et al., 2005). Species with thin, absorptive roots, a high uptake capacity and high maintenance respiration will tend to shed them (Lauenroth et al., 1987; Carmi et al., 1993) or inhibit their growth.

It is important to note that a large number of interacting processes and their complexity can alter root temperature response (Kaspar and Bland, 1992; Faget et al., 2013). Some studies did not consider air and soil temperature independently and, in doing so, confused their effects (Richards et al., 1952; Nielsen and Humphries, 1966). Others did not consider the influence of factors such as phosphorus concentration (Nielsen et al., 1960; Case et al., 1964; Mackay and Barber, 1984), rooting media (Al-Ani and Hay, 1983), shoot temperature or light (McAdam and Hayes, 1981; Rufty et al., 1981; Loffroy et al., 1983; Mackay and Barber, 1984), soil water (Mack and Finn, 1970) and soil strength (Pearson et al., 1970) on temperature response. Fitter et al. (1998) and Edwards et al. (2004) showed that root growth and root respiration rates of different grass species are more closely related to total radiation flux rather than soil temperature, implying that root growth is determined more by resource availability and source-sink relationships within the plants than by close coupling to temperature. Comparison of data and conclusions from different experiments must therefore be considered carefully (Kaspar and Bland, 1992), particularly concerning trees (Faget et al., 2013).

2.2. Soil mechanical properties and soil water stress

When soil is too hard for roots to penetrate, plants encounter the phenomenon of mechanical impedance (Gregory, 2008; Waisel et al., 2002; Bengough et al., 2011). This can be caused by soil compaction, usually associated with heavy farm machinery in arable systems, or by drought and drying soil (Bengough et al., 2011). Compaction is particularly common in poorly structured soils (low presence of aggregates) that include layers of bedrock, iron pans, excessive stoniness, or clay soils (Crow, 2005; Da Silva et al., 1994; Hamza et al., 2007).

Water stress and mechanical impedance are usually considered and studied together (Bischetti et al., 2009) and also closely connected in inhibiting root elongation. As soils dry, capillary forces make matrix potential more negative, often causing soil strength to increase rapidly (Whalley et al., 2005; Whitmore and Whalley, 2009). Mechanical

impedance may be a major limitation to root growth in soil as wet as −100 KPa (−0.1 MPa) due to the increase in effective stress between soil particles from the tension in water films between the particles (Whalley et al., 2005).

However, there is evidence to show that, in some cases, mechanical impedance plays a major role on root elongation as does water stress in others (Taylor and Ratliff, 1969; Mirreh and Ketcheson, 1973; Veen and Boone, 1990; Sharp et al., 1988; Whalley et al., 1998).

For instance, in relatively moist soils (e.g. matric potential of – 0.1 MPa to – 0.2 KPa; no water stress), mechanical impedance can halve root elongation; conversely, in the absence of mechanical impedance, water stress (matrix potential −0.5 MPa; dry soil) can halve root elongation (Bengough et al., 2011).

The literature offers several studies focused on the influence of soil strength on root elongation rate and diameter increase (Sarquis et al., 1991, 1992; Zanetti et al., 2015; Popova et al., 2016; Colombi et al., 2017). The inhibition of root elongation is usually linked to progressive root thickening (Sarquis et al., 1991; Popova et al., 2016). In 2016 Popova et al. found that maize roots grew more slowly (root growth rate (mm h–1); 50% decrease) with increased diameters (root diameter (mm); 15% increase) in denser soils (1.7 vs. 1.5 g cm^{-3}). However, due to variability in the experimental methodology, plant species and soil classification, contrasting results have been produced. Zanetti et al. (2015) uprooted 243 mature trees of 12 species from homogeneous French dikes. Their results showed that in coarse soil materials (dominant particle size between 63 and 0.63 mm) trees develop fewer larger roots. In fine materials (dominant particle size between 0.63 and 0.002 mm, including medium and fine sand, silt, and clay), root systems can have up to three times more roots but they are 40% thinner and shorter.

2.3. Soil air and water transport

Soil mechanical impedance and water content interact to affect root growth. Moreover, as soil becomes more compact (fewer aggregates and less pores in the soil) or water content increases (in the case of waterlogging), oxygen availability becomes a third determinant for root growth (Gregory, 2008). During the growing season, roots use large amounts of oxygen and produce and release large quantities of carbon dioxide into the soil (Woods, 1957). Poor air circulation leads to toxic concentrations of CO_2 and further inhibits plant growth (when oxygen levels rise to 10–15%) or stop altogether (when oxygen levels fall below 3–5%) (Gregory, 2008). The development of a shallow root system is a viable solution in soils with permanently high water tables, but also in cases of drought or sandy soils to maximize rainfall interception near the soil surface (Crow, 2005; Štofko, 2010).

According to Burgess et al. (1998) plant roots affect the distribution and availability of water in the soil profile. Root systems redistribute soil water from deeper layers to dry surface horizons (“hydraulic lift”) while in rainy seasons they transport water from the surface to deeper soil horizons (“hydraulic redistribution”).

2.4. Soil nutrient availability

Root anatomical characteristics are fundamental to understanding how roots grow (Fig. 1) (Eissenstat and Volder, 2005), interact with the soil (Hitz et al., 2008) and uptake nutrients. The primary root of a plant grows as a branched cylindrical organ into the soil (Evert, 2006; Giehl et al., 2013). Secondary roots develop from the primary root in order to find water and nutrients in the soil. The most external part of young roots is the epidermis; it contains root hairs that are microscopic extensions of root epidermal cells in close contact with soil particles which greatly increase the surface area of the root, thus providing a greater capacity for absorption of ions and water from the soil (Taiz et al., 2015; Bibikova and Gilroy, 2003). Conversely, woody roots are not able to absorb substances from the soil due to their external, impermeable covering layers of cork and phelloderm (Gregory, 2008).

Nutrients that are fundamental to complete the plant life cycle and directly involved in its physiological or biochemical functions (Marschner, 1995) are defined as “essentials”. The elements considered as essential for higher plants are: macronutrients (carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S)) and micronutrients (iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B), molybdenum (Mo) and chlorine (Cl)) (Gregory, 2008; Giehl et al., 2013).

Soil nutrient composition can fluctuate widely in space and time (Giehl et al., 2013; Burns, 1980; White et al., 1987), and one of the main factors involved in this process is soil water content (Wild, 1988). Soil water content influences the chemical balance between solid and liquid phases, and the process of organic matter mineralization. The dynamic composition of the soil solution encourages plant growth while modifying their root system architecture to maximize nutrient absorption (Giehl et al., 2013; Burns, 1980; White et al., 1987).

Plant roots respond to the spatial and temporal variations in resource supply (Burns, 1980; White et al., 1987) with a wide range of morphological and/or physiological reactions (Hodge, 2003).

The morphological plasticity of tree roots is defined by measuring the specific root length (Vuuren et al., 1996; Hodge et al., 1999; Larigauderie and Richards, 1994; Farley and Fitter, 1999), root demography (Gross et al., 1993; Pregitzer et al., 1993; Hodge et al., 1999) and biomass allocation (Grime, 1979; Chapin, 1980; Grime et al., 1986, 1991; Reynolds and D’antonio, 1996; Robinson and van Vuuren, 1998; Gärtner and Bräker, 2004). However no single criterion has proved definitive perhaps because the root system response is strictly correlated to the specific environmental context, making generalizations difficult (Hodge, 2004).

In addition to root morphological responses, physiological alterations in uptake capacity can play an important role in nutrient acquisition. Increased uptake may be caused by a higher uptake capacity or a higher ion affinity of the roots or, more simply, an increase in nutrient (substrate) concentrations (Hodge, 2004).

Furthermore, roots with a specialized morphology and physiology known as cluster roots are able to maximize P acquisition from soils with low P availability, particularly when it is present in insoluble complexes (Lambers et al., 2008; Skene et al., 1998). According to Lambers et al. (2008) cluster roots are “bottle-brush-like or Christmas-tree-like structures in roots with a dense packing of root hairs; these structures release carboxylates into the rhizosphere, thus solubilizing poorly available nutrients (e.g. P)”.

The movement of nutrients from the bulk soil to the root surface occurs through processes of mass flow and diffusion. Mass flow (convection) occurs as a result of transpiration; dissolved ions are carried to the root surface in the hydraulic continuum formed by the soil–plant–atmosphere (Tyree, 2003; Gregory, 2008). Several experiments have been carried out on crops (maize, Barber et al., 1963; leek, Brewster and Tinker, 1970; winter wheat, Gregory et al., 1979) and trees (beech, Prenzel, 1979) to estimate the amount of nutrients obtained by the plant thanks to mass flow. The results show that, in general, mass flow will transport more than sufficient amounts of S, Ca, Na and Mg to the root surface (although not Ca in the acid soil, pH 4, used by Prenzel, 1979), significant but insufficient quantities of K and N, and insufficient P (Chapin, 1980; Gregory, 2008). Diffusion occurs when ions move along a concentration gradient established between the root surface and the bulk soil; ions diffuse towards the root if they are taken up faster than they are carried to the root surface by mass flow and away from the root if the converse happens (Gregory, 2008).

There is a vast amount of literature on the mineral nutrition of plants and the role of soils in supplying nutrients, however, it is mainly focused on managed crops (e.g. Barber, 1995), seedlings (e.g. Fotelli et al., 2002) and grasslands (e.g. Whitehead, 2000), rather than on adult trees (Marschner, 1995). This is probably due not just to the ease of analysing small plants in a controlled environment but also to the key

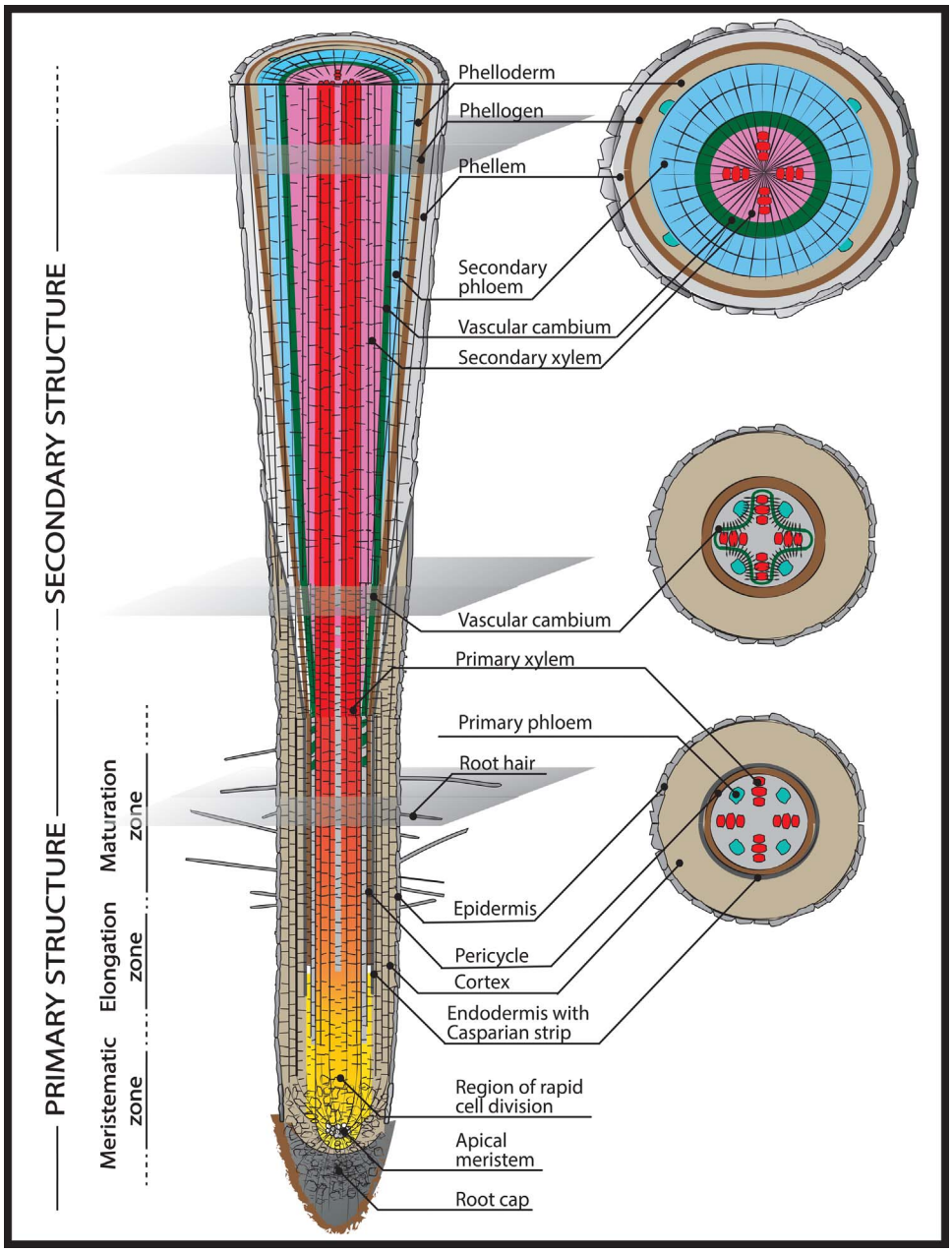

Fig. 1. Longitudinal and transverse section of a terminal root.

role of nutrients in agricultural productivity and food production whichinspire research in this field (Vlek et al., 1997; Tilman et al., 2002; Lynch, 2007; Fageria et al., 2008; Passioura, 1983).

3. Biotic factors and tree roots

The rhizosphere is the narrow region of soil that is directly influenced by root secretions and associated soil microorganisms (Fig. 2) (Blume et al., 2015). Soil organisms, defined as organisms spending part of their life cycle in the soil and interacting with plant belowground organs (Desbrosses and Stougaard, 2011; Robert-Seilaniantz et al., 2011), coevolved with plants, becoming more or less strong selective constraints (Puga-Freitas and Blouin, 2015).

The starting point for physical and biological interactions between plants and soil organisms is the release of organic carbon by the plant roots, termed rhizodeposition (Jones et al., 2004; Walker et al., 2003). Rhizodeposition includes: (1) root cap and border cell loss, (2) death and lysis of root cells (cortex, root hairs, etc.), (3) carbon flow to root-associated symbionts living in the soil (e.g. mycorrhizas), (4) gaseous losses, (5) leakage of solutes from living cells (root exudates, fuelling mainly free-living rhizobacteria), and (6) insoluble polymer secretion from living cells (mucilage) (Jones et al., 2009; Bonkowski, 2004). The carbon pulses stimulate the activity of fast-growing bacteria, actinomycetes and fungi (Semenov et al., 1999; Hodge et al., 2009). Signal molecules are produced by soil organisms and collected by plant receptors at the level of root tips. These molecules interact with plant hormone transport and signalling pathway and may induce development or immunity. Feedback loops may increase or diminish the force of microorganism signals and influence the plant responses. Root exudates feed microorganisms that biodegrade organic matter and free nutrients for plants (Andreetta et al., 2013; Barot et al., 2007; Fontaine et al., 2003; Havlicek and Mitchell, 2014; Kuzyakov, 2010; Nardi et al., 2005; Ponge, 2005, 2013; Six et al., 2004).

Modifications of several plant developmental processes in response to soil organisms have largely been reported for root: root ratio, root system structure via root elongation, lateral root emission and

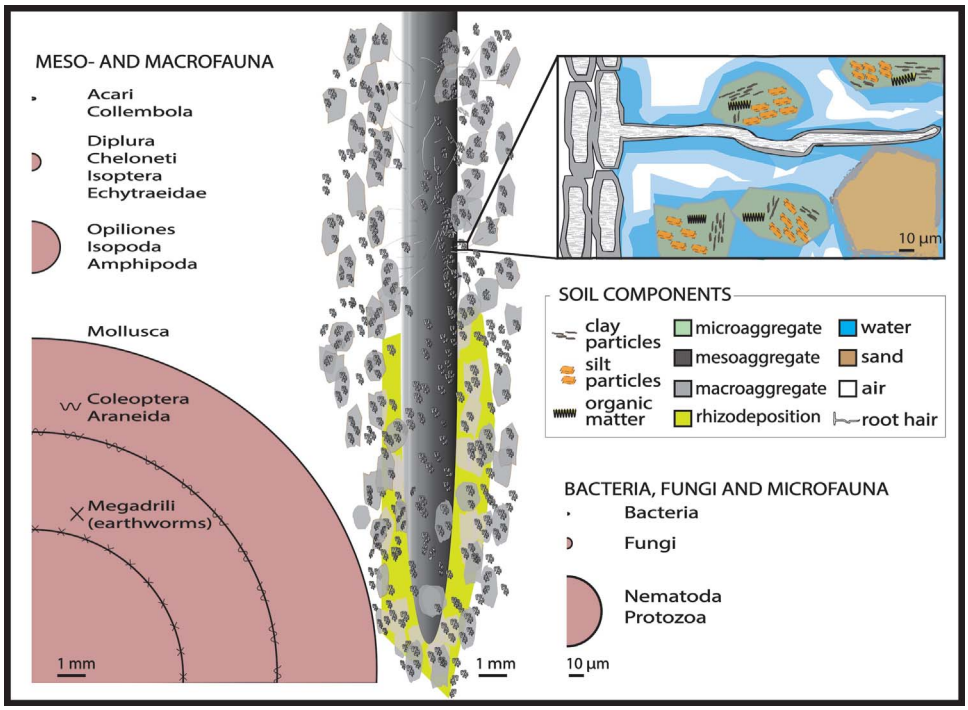

Fig. 2. Root rhizosphere: dimensional relationships between a terminal root, soil organisms (meso and macrofauna at the bottom left, fungi and microfauna bottom right), and soil particles. Average body size of soil organisms according to Anderson et al. (1979) and Paul (2014).

elongation, shoot morphology via leaf area, mass per unit area, floral stem height, grain yield, seedling emergence and vigour (Blouin et al., 2007; Grunewald et al., 2009a; Jana et al., 2010).

Recent discoveries (Andreetta et al., 2016; Fusaro, 2015; Lowenfels, 2017; Lewis and Lowenfels, 2010; Martinez-Salgado et al., 2010; Pey et al., 2014; Puga-Freitas and Blouin, 2015) highlight the central role of soil organisms in plant growth. It was believed that for growing plants, it was necessary to feed them directly, as we do with animals. We now know that it is much better to feed the soil organisms. Soil organisms interact with plants and finally lead to the development and evolution of a "plant and soil" system.

This section aims to list and describe the most important soil organisms according to their physical association with plants (Puga-Freitas and Blouin, 2015) in order to clarify the main agents of nutrient cycling in the soil and how plant roots growth is involved in this process.

3.1. Root physically associated organisms

3.1.1. Symbiosis and pathogenic bacteria

The symbiotic association of Fabaceae plant species with *Rhizobium* is a well-investigated interaction (Desbrosses and Stougaard, 2011; Ferguson and Mathesius, 2003; Oldroyd and Downie, 2008; Long, 1989; Masson-Boivin et al., 2009). The interaction results in visual symptoms, with the formation of nitrogen-fixing nodules. Nodules are specialized root organs in which symbiotic bacteria (Rhizobia) are able to convert atmospheric nitrogen (N_2) into ammonia as a nitrogen source (Hodge et al., 2009). Reciprocally, plants provide a carbon source for *Rhizobium* strain (Puga-Freitas and Blouin, 2015).

In contrast to *Rhizobium* whose interaction with plants leads to a symbiotic association, other bacteria such as *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes* are pathogenic and their association with plants results in the development of tumours or galls (Holsters et al., 1978; Puga-Freitas and Blouin, 2015). Tumour or gall formation induced by *Agrobacterium* strains involves transfer of T-DNA from bacteria into the genome of infected host cells (Spaepen et al., 2007).

3.1.2. Root associated and pathogenic fungi

In contrast with the symbiosis with *Rhizobium*, a large number of plant taxa are able to establish symbiotic association with mycorrhizal (literally meaning 'fungus-root') fungi (Hodge et al., 2009; Puga-Freitas and Blouin, 2015).

The most widespread symbiotic association among plants, which affects about 82% of plants in natural, agricultural and forest ecosystems (Brundrett, 2002; Smith and Read, 2010), are arbuscular mycorrhizae (AM) and ecto-mycorrhizae (ECM). Finely branched hyphae of AM colonize cortex cells by forming arbuscles (Hodge et al., 2009). AM extensive mycelial development can scavenge inorganic P and inorganic N and transport them to the root system over relatively long distances (up to 25 cm has been measured) (Smith et al., 2008). However, the AM fungi probably have a rather low capacity to release nutrients either from sorbed inorganic forms or from organic combination. Citing Lambers et al. (2008) "they 'scavenge' but do not 'mine' the soil".

Whereas, ECM colonize the root cell intracellularly and intercellularly, covering the root apices with a fungal mantle (sheath), from which hyphae extend into the soil. The sheath inhibits the creation of root hairs, which are very few or absent (Hodge et al., 2009). The fungus mycelium always remains apoplastic (intra cells) and can colonize the epidermal (angiosperms) and cortical (gymnosperms) layers, forming the Hartig net, a complex branched structure, which mediates nutrient transfer between fungus and plant (Smith and Read, 2010). ECM are able not just to take up inorganic nutrients from the soil solution (scavenging capacity) but also, due to hydrolysis, to release phosphorus and nitrogen from organic forms (mining capacity) (Lambers et al., 2008).

In the natural environment being mycorrhizal is the norm rather than the exception (Hodge et al., 2009). When a nutrient depletion zone develops around the roots, in order to survive, plants create a symbiosis with fungal hyphae that are able to extend out from the depletion zone and explore a larger soil volume for nutrients acquisition. Once the fungi find nutrients they exchange them with the plant for carbon exudates. The exchange of phosphate and the capture mechanism is well studied (Brundrett, 2002; Smith and Read, 2010); conversely the exchange of nitrogen (Govindarajulu et al., 2005; Hodge et al., 2001; Read and Perez-Moreno, 2003) and the capture of nitrogen from the complex patches still needs to be defined (Smith and Read, 2010).

However, some mycorrhizal species undergo a direct transition to a parasitic mode of living, where the fungus damages or kills the plant

(Blume et al., 2015). These fungi are called pathogens; they reduce plant growth and affect root architecture (Hodge et al., 2009).

In conclusion, mycorrhizal fungi are a fundamental plant symbiont, able to alter their species composition not just according to the stages of soil development (Lambers et al., 2008) but also according to tree age (Dighton and Mason, 1985; Dighton et al., 1986; Gardes and Bruns, 1996) and health (Montecchio et al., 2004). Ecological research on mycorrhizae up till now has favoured laboratory and greenhouse studies (Klironomos and Kendrick, 1993), as opposed to in the field (Bast et al., 2014, 2016).

3.1.3. Root associated microfauna

Soil animals up to 100 µm in size are known as microfauna. The main taxonomic groups are Nematodes and Protozoa (Decaëns, 2010). Nematodes can colonize plant roots, suppress plant defences, or promote the formation of nematode feeding sites (Haegeman et al., 2012; Grunewald et al., 2009a,b). These feeding sites allow the development of either a gall in plant tissues, or a cyst located outside root tissues, derived from the body of the adult nematode (Puga-Freitas and Blouin, 2015). The new generation then emerges from these structures (Barker et al., 1998).

Pathogenic protozoa are responsible for club-root disease (formation of aberrant roots) (Ludwig-Müller and Schuller, 2008). There is a lack of literature on the effects (beneficial to deleterious) of these organisms on plant development (Puga-Freitas and Blouin, 2015).

3.2. Free-living organisms

In contrast to previously described organisms that are closely associated with roots, these are soil organisms which do not penetrate root tissue. Larger organisms other than bacteria and fungi belonging to micro-, meso- and macro-fauna living in soil or litter can interact with plants by emitting hormonal signals from a distance (Puga-Freitas and Blouin, 2015). Such interactions can have either a positive effect on plants, and are called plant growth promoting bacteria/rhizobacteria or fungi (PGPB/PGPR and PGPF, respectively) (Bashan and Holguin, 1998; Contreras-Cornejo et al., 2009; Schroth and Kloepper, 1978), or a negative effect, and these are known as the deleterious rhizobacteria (DRB) (Nehl et al., 1997). The distinction between DRB and PGPR is fine and porous: some PGPR could act as DRB according to plant host genotype, soil environmental factors and time (Nehl et al., 1997).

3.2.1. Microfauna

Microfaunal grazers, particularly protozoa (Bonkowski, 2004) and nematodes, strongly regulate the amounts of microbial biomass and activity in the rhizosphere. The interaction between bacteria, fungi and their microfaunal grazers, triggered by the release of root organic carbon, is known as the 'microbial loop in soil' (Clarholm, 1985); it affects the nutrient cycling rate and strongly enhances the availability of mineral nutrients to plants (Ingham et al., 1985; Gerhardson and Clarholm, 1986; Ritz and Griffiths, 1987; Kuikman et al., 1990; Jentschke et al., 1995; Alphei et al., 1996; Bonkowski et al., 2000a,b; Gregory, 2008; Ekelund and Rønn, 1994; Griffiths, 1994; Christensen et al., 1992; Griffiths and Caul, 1993; Griffiths et al., 1993; Zwart et al., 1994). The microbial loop provides strong evidence of the importance of protozoan and nematode grazing in the food-web models (Clarholm, 1985; Griffiths, 1994; Zwart et al., 1994; Bonkowski, 2004), concluding that they are one of the most important contributors to nitrogen mineralization (Hunt et al., 1987; De Ruiter et al., 1993; Schröter et al., 2003).

In particular, nematodes and protozoa graze on soil microorganisms in the rhizosphere (Kaye and Hart, 1997; Jingguo and Bakken, 1997), liberating NH_4 (ammonia). Nitrifiers and IAA producing bacteria intercept NH_4 and release NO_2 and IAA in the soil, which is then used by the plant for its growth (Blume et al., 2015). Barker et al. (1998) reviewed 27 papers in their monograph exploring nematode biology, systematics and ecology.

3.2.2. Mesofauna

Soil organisms varying in size between 100 µm and 2 mm belong to the mesofauna (Decaëns, 2010). The main taxa are Acari, Collembola, Diplura, Symphyla, Enchytraedae, Isoptera/Formicoidea and Diptera. The effect of these organisms on plant growth has rarely been studied (Puga-Freitas and Blouin, 2015), except for collembolans (Endlweber et al., 2011).

3.2.3. Macrofauna

Soil animals above 2 mm in size are called macrofauna (Decaëns, 2010). This category comprises Isopoda, Myriapoda, Arachnida (e.g. Opiliones), Coleoptera, Mollusca, Oligochaeta (such as earthworms) and Insecta (such as ants and termites) (Decaëns, 2010; Lavelle and Spain, 2001). There have been relatively few studies carried out on macrofauna, with the obvious exception of earthworms (see Scheu (2003) for plant response to the presence of earthworms).

The processes by which macrofauna affect root growth are generally poorly understood. They usually include, in the long term, the changing of soil structure due to the mineralization of soil organic matter that makes nutrients available to the plant (Blouin et al., 2013; Brown et al., 2004) and in the short term, the production of growth-promoting compounds such as IAA and dispersal of growth- stimulating and anti-pathogenic microbes (Puga-Freitas et al., 2012; Gregory, 2008).

4. Functions of tree roots

4.1. Soil stabilization

Tree roots can increase soil stability by improving its mechanical and hydrological properties (Gray and Sotir, 1996). To quantify the contribution of roots to soil stabilization the most commonly considered root traits are root morphology, tensile strength, depth, diameter, biomass and length density. The contributions of roots to erosion control and slope stability depend on root properties (Styczen and Morgan, 1995; Wu, 1995) and their association with mycorrhiza (Bast et al., 2014). Shallow, densely distributed roots play a significant role in erosion control by enmeshing soil particles (Jastrow, 1987) and reducing runoff velocity (Reubens et al., 2007). Roots also increase soil permeability (Vergani and Graf, 2015), which means greater water infiltration. Root-derived organic matter binds soil particles and stabilizes micro-aggregates (Amezketa, 1999).

Deep and densely distributed root systems can further contribute to slope stabilization by increasing soil shear strength when traversing soil layers (Ziemer, 1981). Larger size roots (> 20 mm in diameter) act mainly as individual anchors and contribute less to soil reinforcement (Reubens et al., 2007; Bischetti et al., 2005) while finer roots (1–20 mm in diameter) are more flexible and more able to utilise their maximum tensile strength before breaking in tension (Styczen and Morgan, 1995). Deep and densely distributed roots can reduce the soil water content through evapotranspiration thereby helping prevent oversaturation (Wu, 1984). However, increased soil permeability, oversaturation and increased water pressure seepage can lead to slope failure (Cammeraat et al., 2005).

4.2. Phytoremediation

Trees can also be effective biological filters in the process of removing organic or inorganic contaminants from the soil (Blaylock, 2000; Alkorta and Garbisu, 2001) and water (Salt et al., 1995). The mechanism is based on the hydraulic uptake of the tree. Once contaminants are taken up by the root system of the tree, they become either locked in the plant tissue or are processed into less toxic materials (Ghosh and Singh, 2005). The deeply penetrating, elaborate root system of trees with high water uptake capacity and intense growth can play a major role in phytoremediation (Pulford and Watson, 2003). A number of studies have also highlighted the side effects of

phytoremediation on the number and composition of soil fauna (e.g. Römkens et al., 2002).

4.3. Carbon sequestration

Removing carbon dioxide from the atmosphere is a pressing issue. Vegetation plays a major part in this process. Through tree roots a large amount of carbon can be stored in the soil each year (Bast et al., 2016). Root delivered carbon is more likely to be assimilated than shoot delivered C (Rasse et al., 2005) due to the physico-chemical interactions between roots and soil particles. Soil organic carbon in deeper soil horizons hugely relies on the input of root delivered carbon. The turnover rate of fine roots is one of the determining factors of the carbon units a tree can sequester though some species (e.g. pines) have a slower turnover rate of fine roots (4.2–12 years) compared to others like sweetgum tree (1.25–4 years) (Argonne National Laboratory, 2005). This implies that tree species with fine roots having a shorter lifespan are able to stock a higher amount of organic matter and more carbon in the soil layers than species with a longer lifespan (Argonne National Laboratory, 2005). The form of mycorrhiza interactions related to the root system of trees can alter the rate of carbon that can be sequestered in the soil by up to 70%, independently of temperature, precipitation, soil clay content as well as biomass accumulation (Averill et al., 2014). A number of trees with a deep root system are able to indirectly act on a greater level of carbon accumulation in the soil due to their hydraulic redistribution ability (University of California-Berkley, 2006). Redistributing water from the deeper layers during the dry season would allow the plant to continue its photosynthesis and take up more carbon from the atmosphere.

5. Conclusions

Root systems are able to grow in a heterogeneous soil environment, modifying their architecture according to water and mineral nutrient availability (Malamy, 2005), physical obstacles, soil properties (Popova et al., 2016) and creating mutualistic associations with key soil microorganisms. To reduce the variability of the surrounding environment and facilitate the detection and exclusion of confounding factors, these interactions have mainly been studied on seedlings or crop plants in controlled growing conditions (Gregory, 2008).

It is still astonishing how much we do not know about tree roots and their growth and development (Espeleta et al., 1999; Fernández et al., 1991). The challenge is not only to understand how tree roots function but to do so in soil with all its physical, chemical and biological complexity (Ryan et al., 2016). It is definitely difficult to study roots in situ, especially for trees. However, the lack of knowledge in this field of botanical research is so gaping that we call for scientists from varying disciplines to combine their expertise and efforts to design tools, investigation techniques and methods to address research questions on tree root systems in situ and their variations in a broad ecological sense.

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