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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

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