



Review paper

Root exudates mediated interactions belowground



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ABSTRACT

The root exudate composition reflects the contradictory-concomitantly attractive and repulsive-behaviour of plants towards soil microorganisms. Plants produce antimicrobial, insecticide and nematicide compounds to repel pathogens and invaders. They also produce border cells that detach from roots and play an important role as biological and physical barrier against aggressors. Plants produce also metabolites used as carbon source resulting in the attraction of phyto-beneficial soil microorganisms that help plants in controlling diseases directly via the production of antimicrobial compounds or indirectly via the induction of plant systemic resistance. The root exudates may have a direct impact on carbon and nitrogen cycling, as they exhibit a rhizosphere priming effect towards soil organic matter degraders, and may inhibit nitrification process by soil nitrifying microorganisms. They also contain signalling molecules required for the establishment of 'plant-microorganisms' interactions. The composition of root exudates is therefore broad ranging, consisting of feeding, antimicrobial and signalling molecules. We thus focused this review on current research concerning the role of the root exudate composition in 'plant-microorganisms' interactions and functioning of the rhizosphere.

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1. Introduction

The rhizosphere is best defined as the volume of soil around living roots, which is influenced by root activity (Hiltner, 1904). This is a densely populated area in which plant roots must compete with the invading root systems of neighbouring plants for space, water and mineral nutrients, and with other soil-borne organisms, including bacteria, fungi and insects feeding on the abundant source of organic material (Ryan and Delhaize, 2001; Bais et al., 2004a).

The ability to secrete a wide range of compounds into the rhizosphere is one of the most remarkable metabolic features of plant roots, with around 5–21% of total photosynthetically fixed carbon being transferred into the rhizosphere through root exudates (Whipps, 1990; Marschner, 1995; Nguyen, 2003; Derrien et al., 2004). The quantity and quality of root exudates depend on

the plant species, the age of individual plants and external biotic and abiotic factors (Jones et al., 2004).

Root exudates are often divided into two classes of compounds: i) low-molecular weight compounds such as amino acids, organic acids, sugars and other secondary metabolites, which account for much of the root exudate diversity, whereas ii) high-molecular weight exudates, such as mucilage (polysaccharides) and proteins, account for a large proportion of root exudates in terms of mass (Badri and Vivanco, 2009).

Through the exudation of a wide variety of compounds, roots may regulate the soil microbial community in their immediate vicinity, cope with herbivores, foster beneficial symbioses, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species (Nardi et al., 2000; Walker et al., 2003). Indeed, in addition to providing a carbon- and energy-rich environment, plants recognize and actively respond specifically to different microorganisms encountered in the rhizosphere, initiating communication with soil microbial communities by producing signals that modulate colonisation. Plants mediate both positive and negative interactions in the rhizosphere via root exudates (Bais et al., 2006; Philippot et al., 2013). The positive interactions include symbiotic associations with beneficial microbes, such as rhizobia,

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mycorrhiza and plant growth promoting rhizobacteria (PGPR). Negative interactions include associations with parasitic plants, pathogenic microbes and invertebrate herbivores.

Here we review the large body of literature that has been published on root exudates and their interaction with soil organisms, while assessing current knowledge related to how plants, via root exudates, mediate communication with microbial communities in the rhizosphere.

2. Rhizodeposition concept

For over a century it has been known that plants can dramatically modify their soil environment through the release of carbon compounds (rhizodeposition) from living plant roots, giving rise to the so-called rhizosphere effect (Hiltner, 1904). The release of carbon (C) from root epidermal and cortical cells leads to a proliferation of microorganisms within (endorrhizosphere) or on the root surface (rhizoplane), and outside the roots (ectorrhizosphere) (Jones et al., 2004). The rhizosphere may contain up to 10^6 – 10^9 bacteria, 10^4 protozoa, 10^1 – 10^2 nematodes and 10^5 – 10^6 fungi per gram of rhizosphere soil (Watt et al., 2006; Hinsinger et al., 2009; Mendes et al., 2013).

The C release in the rhizosphere leads to chemical, physical and biological characteristics that differ from those of the bulk soil (Barber and Martin, 1976). The magnitude of these changes in soil properties is largely determined by the amount and type of C release from the roots, as well as intrinsic soil characteristics (Jones et al., 2004; Alami et al., 2000).

The amount of carbon exuded by plants has been quantified relatively easily in the absence of soil by growing roots in sterile hydroponic culture and collecting the carbon accumulating in the external media (for review, Nguyen, 2003). However, this method lacks ecological relevance (Jones et al., 2009).

The introduction of tracer techniques for labelling of root-derived C has led to significant progress of the estimation of C input into soil (Jones et al., 2009). For example, Kuzyakov and Domanski (2000) estimated that cereals (wheat and barley) and pasture plant transfer 20–30% and 30–50% of total assimilated carbon into the soil respectively. Derrien et al. (2004) estimated to 16% the C input into the soil by wheat plant using ^{13}C labelling for 5 h.

Different rhizodeposit nomenclatures have been proposed based, for instance, on the mechanisms of release, biochemical nature or functions of rhizodeposits in the rhizosphere (Jones et al., 2009).

Exudates

Root exudates are part of the rhizodeposition process, which is the major source of soil organic carbon released by plant roots (Hutsch et al., 2000; Nguyen, 2003). Exudates are defined as soluble low-molecular weight components which are lost simply through passive diffusion and over which the plant exerts little control (basal exudation) (Bertin et al., 2003; Bais et al., 2006). These exudates include amino acids, organic acids, sugars, phenolics and other secondary metabolites. Their concentration inside roots is typically many orders of magnitude greater than in the surrounding soil solution due to continual removal from the soil by the soil microbial community and replenishment of internal pools by the roots (Jones et al., 2009).

Mucilage

Root mucilage forms a gelatinous layer surrounding root tips and is one of the few clearly visible signs of organic C excretion

from roots (Jones et al., 2009). This substance is mainly composed of polysaccharides, proteins and some phospholipids (Read et al., 2003). In most situations, mucilage released into the soil has a wide range of benefits for plants, such as protecting the root meristem from toxic metals, enhancing soil aggregate stability, which in the long run promotes soil aeration, root growth, prevents soil erosion and maintains a continuous water flow towards the rhizoplane (Read et al., 2003). The amounts of mucilage synthesized *in vitro* range from 11 to 47 $\mu\text{g dm/mg root dm}$ (Nguyen, 2003). However, these quantities were determined from roots grown in water or in nutrient solution, which increases the outward diffusion of the mucilage from the periplasmic region (Sealey et al., 1995). At the present time, to our knowledge, the amount of mucilage produced in soil remains unknown.

Border cells

Many plants can produce large numbers of metabolically active root “border cells”, which are programmed to separate from each other and to be released from the root cap periphery into the external environment (Hawes et al., 2000; Stubbs et al., 2004). Experimentally, border cells can be released into suspension by brief immersion of the root tip in water (Hawes and Brigham, 1992). The separated cells adhere to the root tip in the absence of free water. The daily rate of border cell production is highly variable among plant species, from a dozen in tobacco to more than 10,000 cells/day for cotton and pine, with release rates being highly dependent upon the prevailing environmental conditions (Hawes and Brigham, 1992).

Gases such as ethylene, CO_2 and H_2

Plant roots release CO_2 into the soil environment from carbohydrate respiration and stimulation by lumichrome, a plant and bacterial exudate molecule (Phillips et al., 1999). These accumulations are up to 17.5% in the root zone and increased levels of CO_2 can enhance the dissolution of soil CaCO_3 to produce Ca^{2+} for plant uptake (Dakora and Phillips, 2002).

Hydrogen gas (H_2) is a major byproduct of N_2 fixation in legumes, and its production consumes about 5% of net photosynthesis (Dong and Layzell, 2001). Some rhizobia possess genes encoding for an uptake hydrogenase (Hup) enzyme, which enables H_2 to be oxidized by the bacteria to yield more energy. However, many symbioses, lack this uptake hydrogenase (Hup^-), and the H_2 produced by the nitrogenase diffuses out of the nodule into the soil (Golding et al., 2012). This H_2 loss from nodules to soil is traditionally considered as a disadvantage in Hup^- versus Hup^+ symbiosis. However, the release of H_2 from nodules alters soil biology and may indirectly contribute to plant growth (Dong and Layzell, 2001; Dong et al., 2003). Indeed, the presence of H_2 stimulates the soil H_2 -oxidizing bacterial community that may foster plant growth promotion through various mechanisms such as the increase of root elongation by decreasing ethylene levels in the host plant (Golding et al., 2012), and their presence is beneficial to leguminous and non-leguminous plants (Maimaiti et al., 2007).

2.1. Factors affecting rhizodeposition pattern

Biotic and abiotic factors affecting the release of C from the roots into the soil are numerous and have been extensively reviewed (Whipps, 1990; Jones et al., 2009). For example, the enormous plasticity of root growth and root exudation in response to different soil conditions and particularly to stress factors, such as nutrient limitation, mineral toxicities, and extremes in soil moisture and soil

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