Special Issue: Unravelling the Secrets of the Rhizosphere

Review

Engineering the Rhizosphere

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All components of the rhizosphere can be engineered to promote plant health and growth, two features that strongly depend upon the interactions of living organisms with their environment. This review describes the progress in plant and microbial molecular genetics and ecology that has led to a wealth of potential applications. Recent efforts especially deal with the plant defense machinery that is instrumental in engineering plant resistance to biotic stresses. Another approach involves microbial population engineering rather than single strain engineering. More generally, the plants (and the associated microbes) are no longer seen as 'individual' but rather as a holobiont, in other words a unit of selection in evolution, a concept that holds great promise for future plant breeding programs.

Trends

All components of the rhizosphere (plants and microbes) can be engineered and soil can be amended to promote plant health and growth, from the field to the landscape scale.

Plant engineering has led to valuable results in terms of resistance to high metal concentration in soil and resistance to pathogens, in this latter case in relation with remarkable progress in the understanding of plant defense reactions.

Aside from plant growth promoting rhizobacteria living at the root surface, endophytic bacteria are receiving renewed attention because they have proved to be of interest particularly in the context of tolerance to pollutants.

A novel aspect of microbial engineering involves population engineering rather than single strain engineering.

In relation to what is observed in the animal world, the vision of the plant and its associated microbial cortege is changing; they are not separate elements but rather constituents of a superorganism, the holobiont.

The Rhizosphere: A Place for Complex Plant–Soil–Microbe Interactions

Since the early work by Hiltner (1904) the rhizosphere has been described as the soil compartment that is influenced by plant growth. This influence results from the release by the plant of organic materials, a phenomenon called rhizodeposition, that consists mostly of plant metabolites (the exudates) and plant debris (dead cells, loss of mucilage, etc.; reviewed in [1]). This loss of carbon represents a substantial part of the photosynthetically fixed carbon (from 20% to 40%) allocated to the underground root system (reviewed in [2]). As a consequence, while most bare soils are regarded as **oligotrophic environments** (see Glossary), rhizosphere soils are described as **mesotrophic**, favoring the growth of populations of bacteria, archaea, microbial viruses, and fungi ([3,4] for review). The selected microorganisms exert numerous effects on the plant and overall on rhizosphere functioning. They are part of the carbon cycle, either by recycling carbon molecules or acting as prey for other microbes or larger organisms such as amoebae or nematodes, they may favor plant growth, protect the plant from pathogens, and some may also be plant pathogens. As a consequence of microbial activity, plant rhizodeposition may change qualitatively and quantitatively, affecting in turn the microbial component. This can be described as the characteristic rhizosphere feedback loop that maintains the rhizosphere in a dynamic equilibrium. Such an intricate relationship suggests that the rhizosphere can be engineered to favor plant growth and health, or to limit the consequences of various stresses of biotic or abiotic origins, a feature of major interest in the current context of global climate change and the need for more sustainable agricultural practices (Figure 1). Basically, all three components of the rhizosphere can be manipulated. The soil can be amended to change its physicochemical properties or improve its overall quality, the plant can be engineered to select or introduce a novel trait of interest, and the microbial populations can be selected to promote plant growth and health. In a non-exhaustive way, relevant examples of rhizosphere engineering – and success stories – are given below.

Amending the Soil

Soil amendment dates back at least two millennia. Among the ancient practices of peoples such as the Amerindians, the use of biochar (a fine-grained, highly porous charcoal obtained by pyrolysis of various plant material) allowed the constitution of fertile soils in tropical areas despite

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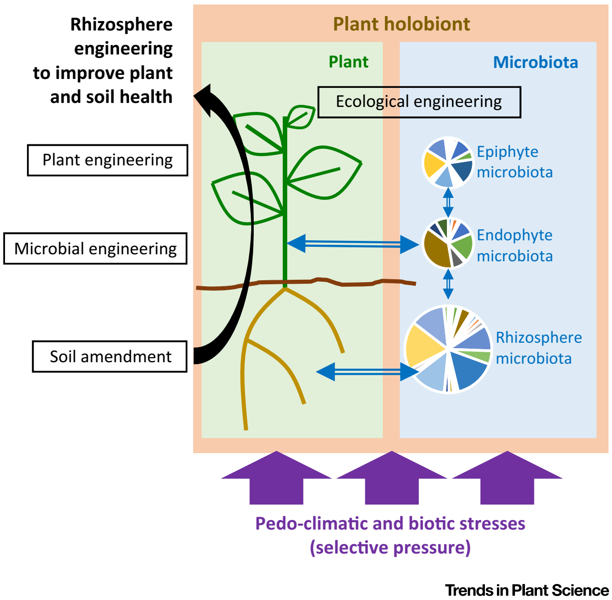

Figure 1. Rhizosphere Engineering Permits Improvement of Plant And Soil Health. Plants are stressed (violet arrows) by pedo-climatic (e.g., high salt or metal concentrations as a result of drought or deforestation) and biotic agents (pathogens). Modification of soil parameters (soil amendments), as well as microbial or plant engineering, are strategies developed to engineer the rhizosphere (blue arrows). Recent approaches involve microbial population (soil, plant, rhizosphere, and endophyte microbiota) engineering rather than single strain engineering, and engineering of the interactions (ecological engineering) between the plant and its associated microbiota (blue arrows). Both the plant (green box) and the associated microbiota (blue box) are now considered as a superorganism, a holobiont (beige box), that is the unit on which the selective pressure applies.

leaching by heavy rains [5]. Indeed, biochar constitutes a source of carbon-rich material, the porous structure of which allows the immobilization of organic compounds, including pollutants ([6,7] for review). Biochar improves the water retention capacity of soils and increases the pH of acidic soils. It also accelerates the decomposition of organic matter in soil by affecting microbial populations [8] and soil pH [9]. This effect is not systematic, and other authors have reported a decreasing organic matter decomposition rate [10], possibly in relation to the origin and composition of the biochar batch.

Aside from classical amendment practices (e.g., biochar or calcic amendments), other methods have been investigated as ways to fight pests or to combine waste management and soil quality. In this line, recent trials with calcium silicate amendment led to a partial control of the sugarcane borer pest, *Diatraea saccharalis*, on rice [11], and the use of plant residues led to partial control of the bacterial phytopathogen *Ralstonia solanacearum* [12]. The use of sewage sludge [13], coal fly ash (a by-product of coal combustion [14]), or cattle manure [15] are well-documented or common despite the associated sanitary concerns (e.g., [16]). Soil amendment remains, however, an empirical technique, even though recent progress in soil analytical tools, microbial ecology, and plant genetics have led to the production of robust – but still descriptive – data (e.g., [17]).

Engineering the Plant

Plant engineering has received considerable attention over the past 30 years, especially with the development of genetic engineering techniques [18]. However, plant engineering goes beyond the currently widely cultivated, genetically modified plants resistant to some insects or tolerant to one or more herbicide families. One very important aspect of plant engineering, often overlooked, deals with tolerance to high metal concentrations. For instance, high aluminium (Al) concentration in acidic soils is a one of the most important factors that affect plant growth in tropical regions, often in relation to deforestation. Several mechanisms underlying Al tolerance in plants have been characterized [19,20]. They can be divided into those that facilitate the exclusion of Al ions from root cells (e.g., the release of some organic acids in the rhizosphere [21,22]) and those that enable plants to tolerate Al once it has entered the cell (e.g., chelation of Al ions by organic substances in the cytosol [23,24]). From these results, efforts have been made to

Glossary

Cryptogamic infections/diseases: infections and diseases that are caused by pathogenic fungi.

Elite cultivars/lines: varieties of a plant (i.e., cultivars) that have been selected intentionally for highly desirable traits, are generally widely cultivated, and are economically profitable.

Holobiont: the term was first introduced to describe a host and its primary symbiont. The definition was next expanded to any close physical association between individuals of different species that occur during significant portions of their life history. All participants are bionts and the resulting assemblage is a holobiont.

Macerating enzymes: enzymes that soften and eventually degrade the plant cell wall. Typical macerating enzymes are pectinases (pectine lyases, pectate lyases), cellulases, and polygalacturonases

Marker-assisted selection: a breeding process whereby a marker, generally a specific DNA sequence, is used for the indirect selection of a genetically linked determinant(s) of a trait of interest (e.g., abiotic stress tolerance, disease resistance).

Mesotrophic environments: environments that can sustain life some extent, and hence are characterized by sufficient amounts of minerals and nutriments, and especially elaborated carbon compounds.

Oligotrophic environments: environments that offer little to sustain life, and hence are characterized by low concentrations of nutriments, especially elaborated of carbon compounds. The opposite are heterotopic (or eutrophic) environments.

Panicle: a branched inflorescence in which each branch has more than one flower. This type of inflorescence is a characteristic of monocots such as oat and rice.

Quantitative trait locus (QTL): a region of genomic DNA associated with a quantitative trait. A quantitative trait is one that varies in a continuous way. For instance, height, root biomass, seed number, protein concentration, etc. are quantitative traits. Note that such traits (that are determined by different loci) are associated with various QTLs.