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Review

Root–Root Interactions: Towards A Rhizosphere Framework

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Plant scientists have made great progress in understanding molecular mechanisms controlling root responses to nutrients of arabidopsis (*Arabidopsis thaliana)* plants under controlled conditions. Simultaneously, ecologists and agronomists have demonstrated that root–root interactions involve more than competition for nutrients. Here, we highlight the importance of both root exudates and soil microbes for root–root interactions, ubiquitous in natural and agricultural ecosystems. We argue that it is time to bring together the recent insights from both scientific disciplines to fully understand root functioning in the real world.

Trends

Many studies have shown the importance of nutrient competition for plant performance in natural and agricultural ecosystems. However, results of several recent experiments show that these interactions cannot be explained by competition for nutrients alone. The rhizosphere has a key role in mitigating root–root interactions.

Both the rhizobiome and root exudation affect root–root interactions either directly or via modification of resource availability to the plants. These pathways are closely connected because exudates affect different components of the rhizobiome, and vice versa.

Combining the toolbox from molecular biology with ecological complexity will elucidate the functional interplay among the rhizobiome, root exudates, and the root, and its importance for plant performance in the real world.

Roots, Resources, and Interactions

In the field, few plants perform as observed in the lab or greenhouse. This is due not only to environmental variability, which tends to be greater in the field, but also to strong interactions with neighbouring plants. Recent work in natural systems and agriculture has shown that these competitive interactions are essential to understand the performance of plants and, consequently, community productivity and crop yield. The classic idea is that plant interactions are driven by resource **competition** (see Glossary). **Resources** (e.g., light or nutrients) that are used by a neighbour are no longer available for the focal plant, inhibiting its performance. Plant responses to light interception by neighbours (i.e., shade avoidance) are well established, from the molecular regulation up to the ecological consequences [1,2]. Recently, great progress has been made in revealing the signalling pathways of roots to different nutrients leading to different root anatomy [3,4]. At the same time, ecologists are making progress in demonstrating that root–root interactions are more specific than can be expected from competition for nutrients alone [5,6]. Consequently, the integrated picture from molecular signalling to plant responses and community consequences is far from comprehensive belowground. One of the challenges for scientists aiming to integrate belowground responses is the fact that the number of resources is greater in the soil than in the canopy. Perhaps a more fundamental issue is that, in contrast to the phyllosphere, interactions among roots and microbes in the **rhizosphere** may enhance the availability of resources. The dense populations of microorganisms in the rhizosphere, the so-called '**rhizobiome**' [7], can directly affect nutrient availability to the plants [8,9]. In turn, the rhizobiome is fuelled by carbon-rich substrates excreted by plants: **root exudates**. Recent evidence suggests also that root exudates affect nutrient availability [10,11]. Here, we review the role of root exudates and the rhizobiome in root–root interactions and explain why these processes should be explicitly incorporated in our investigations of belowground plant–plant interactions.

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Basic Ecological Theory: Belowground Resource Competition

Belowground, plants take up water and about 15 essential minerals. Although water may be strongly limiting plant growth in some environments [12], and micronutrients, such as zinc (Zn) or copper (Cu), can be naturally limiting in some soils [13], the most important elements for plant growth are arguably nitrogen (N) and phosphorus (P). N is an abundant element in the atmosphere (N_2), but in this form it is inaccessible to plants, except for a limited number of plant species that are able to form a **symbiosis** with nitrogen-fixing microorganisms (e.g., legumes and rhizobium bacteria). Almost all N in the soil is present in soil organic matter and soil microbes mineralise ammonium (NH_4^+) and nitrate (NO_3^-) from this organic material via decomposition and mineralisation. This available N pool in the soil is dynamic, with intense competition for N among plants and microbes [14]. In contrast to N, P is a rare element at the scale of the globe and it lacks an atmospheric pool. P is bound in mineral soil fractions and is highly insoluble; its availability largely depends on soil chemistry. However, plant species have developed different ways to acquire P, including special root types releasing root-exuded organic acids and mycorrhizae [15,16].

If nutrients such as N and/or P are limiting resources for plant growth, then the performance of an individual plant will be reduced if neighbouring plants take up these nutrients (Figure 1A, Key Figure). This is the basic mechanism of resource competition that has been shown in numerous experiments (reviewed in, e.g., [17–19]). Plant species clearly differ in their demands for nutrients as well as in their strategies to acquire them, which is reflected by a range of root traits [15,20,21] and competitive strategies. One important strategy is to grow fast to dominate the available space and acquire most of the resources [22,23]. As a consequence, competitive plant species can be characterised by high root growth rate, a high degree of selective root placement in nutrient-rich patches [24], and high root turnover [25]. The alternative theory suggests that competitive species have to be highly efficient in nutrient use to draw down the concentration of the limiting resource(s) below the level at which their neighbours can survive [26]. Recent attempts to bring these two plant competition theories together stress the need to include the spatial and temporal heterogeneity of nutrient supply [27]. In high-nutrient environments, light is a limiting resource. Rapid growth and high nutrient uptake will allow species to successfully compete for light in such environments. However, in nutrient-poor environments, the ability of species to extract and conserve the scarce nutrients may be more important than competition for light. It is important to note that these competitive strategies reflect two major physiological trade-offs: (i) allocation to roots to acquire nutrients and water versus allocation to shoots to capture light [28,29]; and (ii) the trade-off between plant growth and survival. At one end of the latter trade-off, plants are characterised by traits that allow fast growth, but inherently lead to high metabolic rates, susceptibility to herbivory, and high tissue mortality. At the other end of the spectrum, plants have slower growth rates, but are equipped for long-term resource retention by having high tissue densities and low respiration rates, enhancing their lifespan. The traits that enhance their lifespan invest in defence and conservation of acquired resources, such as carbon, N, and P, which allows survival under adverse conditions (i.e., resource economics spectrum) [30,31].

Rather than competing for nutrients, neighbouring plants may also avoid competition via resource use differentiation. The legumes mentioned earlier, which have access to an N pool unavailable to other plants via their symbiosis with N-fixing bacteria, are a well-known example, but nutrient uptake of plants may also differ temporally (phenology [32]), spatially (e.g., differences in rooting depth [33,34]), and in the type of nutrient that is preferentially taken up (e.g., inorganic versus organic N [35,36]). In summary, the traditional view is that plants interact belowground via nutrient competition (Figure 1A).

Belowground Interactions: Beyond Nutrient Competition

Although competition for nutrients is ubiquitous in plant communities, three lines of recent work suggest that root–root interactions are more than just competition for nutrients. The first is the new generation of **mesocosm** experiments on (often pair-wise) competitive interactions

Glossary

Competition: occurs when two individuals interact and perform less than when single grown. Resource competition among plants indicates that resources taken up by one individual are no longer available to the other, thereby decreasing its performance.

Mesocosm: experimental tool to bring part of the natural environment under controlled conditions. In experiments with plants, mesocosms typically refer to small containers.

Mycorrhizae: symbiotic association comprising a fungus and roots of a vascular plant. The plant provides carbohydrate as an energy source for the fungi and receives nutrients (mainly P) from the fungus.

No-tillage management: modern agricultural practice with a reduced number of cultivation steps compared with conventional farming. Successive crops are sown directly into the residue of previous crops without soil or reduced tillage.

Phyllosphere: the aboveground part of a plant that acts as a habitat for microorganisms.

Resource: something in the environment that is taken up by an organism during growth. Relevant belowground resources for plants include nutrients, such as N or P, and water; aboveground resources are light and carbon dioxide.

Rhizosphere: the rhizosphere is the narrow interface between plant roots and soil, where complex interactions between root secretions and associated soil microorganisms occur. These interactions have the potential to affect plant growth, competitive ability, and ecosystem functions, such as nutrient cycling. The term ‘phyllosphere’ is its aboveground equivalent.

Rhizobiome: the microbial community inhabiting the rhizosphere.

Root exudates: the chemical compounds excreted by the plant root. The species-specific chemical signals are involved in the communication between root and the microorganisms present.

Symbiosis: an interaction (positive, neutral, or negative) in which two species exist in intimate physical association for most or all of their lifetime and are physiologically dependent on each other.