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Food for thought: how nutrients regulate root system architecture

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The spatial arrangement of the plant root system (root system architecture, RSA) is very sensitive to edaphic and endogenous signals that report on the nutrient status of soil and plant. Signalling pathways underpinning RSA responses to individual nutrients, particularly nitrate and phosphate, have been unravelled. Researchers have now started to investigate interactive effects between two or more nutrients on RSA. Several proteins enabling crosstalk between signalling pathways have recently been identified. RSA is potentially an important trait for sustainable and/or marginal agriculture. It is generally assumed that RSA responses are adaptive and optimise nutrient uptake in a given environment, but hard evidence for this paradigm is still sparse. Here we summarize recent advances made in these areas of research.

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Introduction

Roots are pivotal for anchorage of land plants in the soil and for efficient uptake of water and mineral nutrients, thus playing a crucial role in plant fitness. The root system is composed of embryonic roots (primary root in Arabidopsis, primary and seminal roots in a few cereal crops) and post-embryonic roots (lateral roots in Arabidopsis, lateral, brace and crown roots in cereals). Root system architecture (RSA), the overall spatial arrangement of individual parts of the root system, is an important factor determining how efficiently plants can access resources. RSA is highly plastic both genetically and environmentally. Thus, different species or ecotypes have evolved different RSAs depending on the prevailing soil conditions. Considerably different RSAs can also be adopted within the same genotype and even within the life span of a single plant because the rate at which individual parts of the root system develop and grow can be altered by short-term environmental signals, including changes in water, nutrient and oxygen availability or pathogens and pests. Unlike animals, plants cannot move away from unfavourable sites. Hence, plant responses to fluctuating soil conditions are based on altered growth and development, and they require sophisticated sensing and signalling mechanisms. While the mechanisms controlling RSA responses to individual nutrients, especially nitrogen (N) and phosphorus (P), have been extensively investigated, the crosstalk between different nutrient signals and the benefits of RSA responses in a particular condition are yet to be characterized systematically. In this review, we will highlight some of the recently identified molecular mechanisms that underpin RSA responses to single and combined nutrient stress, and we will explore the potential benefits of RSA responses for plant performance.

The genetic and environmental context of RSA responses

Most studies into nutrient signalling and RSA have been carried out in *Arabidopsis thaliana* (Col-0) grown on agar plates, and before we review the knowledge generated by these studies, it is important to discuss their transferability to other species and root environments. The endogenous developmental programmes underpinning RSA differ between plant species (especially between monocots and dicots) which is apparent in different RSAs under identical nutrient sufficient conditions. Therefore, a RSA phenotype produced in response to a particular nutritional stimulus can differ between species even if the signalling pathway feeding into the different developmental programmes is conserved. Furthermore, the phenotypic consequence of a change in nutrient supply in a given genotype will depend on exact nutrient concentration, nutrient distribution and gradients, concentrations of other nutrients, developmental stage of the plant, and any factors that determine plant growth rate and nutrient demand, for example, light, humidity, etc. [1•,2•,3]. Differences in these factors are likely to explain many of the discrepancies between studies carried out with the same genotype, for example, *A. thaliana* Col-0. Clearly one has to be careful when drawing wider conclusions from observations made in a specific genotype or environmental condition. However, this does not imply that meaningful data can only be derived from field-based studies on crops. Ultimately, whether findings can be translated between species and environments or not depends on the question posed. If the RSA itself is the focus of interest (e.g. as a trait to enhance agricultural yield or as a phenotype to solve specific developmental questions) the precise experimental context is of essence and findings may not be transferable to other genotypes or environments. If, however, RSA responses are used as readout to enable the identification of nutrient sensors and signalling components, the context is less crucial, and artificial conditions are often more informative than natural conditions. Figure 1 exemplifies the usefulness of Arabidopsis RSA developing on an agar surface for reporting the action of nutrient-specific sensing and signalling pathways. Each specific nutrient treatment leads to a distinct multifactorial phenotypic output that can be interrogated through genetic, pharmacological and physiological manipulations. In the following, we will describe the latest insights that have been obtained using this latter approach.

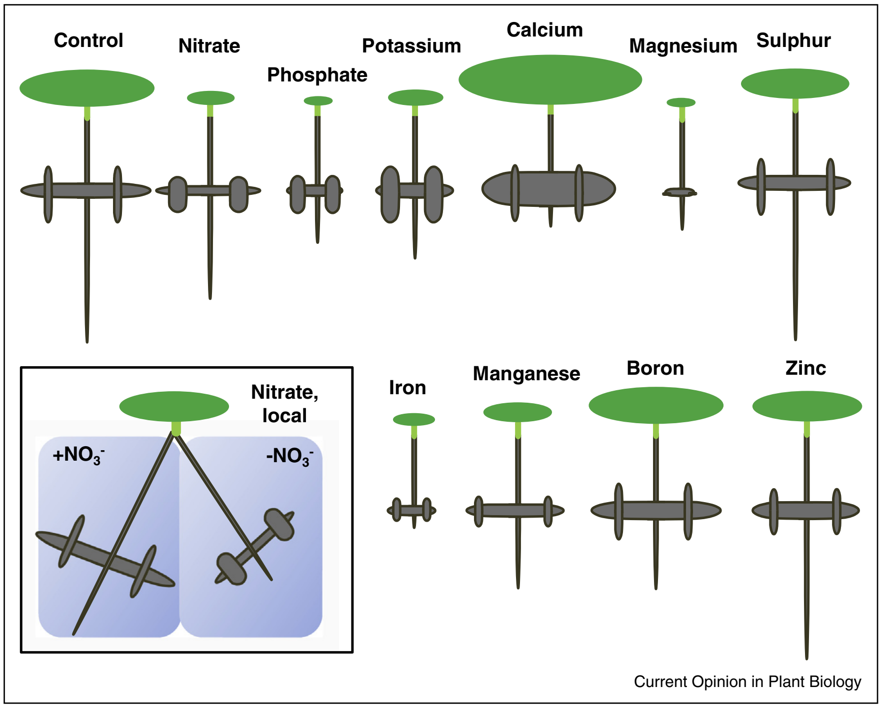
Root system architecture responses to individual nutrients

Nitrate

In Arabidopsis plants grown with uniform nutrient supply, the dose–effect curve for nitrate and lateral root (LR) length is bell-shaped, whereas primary root (PR) length is continuously inhibited by lowering nitrate over the same concentration range [4]. The effect of nitrate on LR initiation is controversial; several studies report a positive effect of nitrate on LR density [5,6] while others have found no effects of nitrate on LR number or density [7]. Non-uniform, localized nitrate supply stimulates LR elongation in nitrate rich patches [3].

NITRATE TRANSPORTER 1.1, NRT1.1 (NPF6.3), is a plasma membrane nitrate transporter that alters its affinity depending on nitrate availability, and functions as a nitrate sensor upstream of transcriptional low-nitrate responses [8]. It also acts as a basipetal auxin transporter in the developing LR tips thereby controlling both local and systemic LR responses to low nitrate [3,9]. Phosphorylation of NRT1.1 at T101 is important for auxin transport activity and for repression of LR emergence in low nitrate (Figure 2) [10•]. A recent study [11] resolved the longstanding question how such a function is compatible with the observed transcriptional down-regulation of NRT1.1 under low nitrate, both at the whole root level and in LR primordia [3,12]. Bouguyon and colleagues showed that in contrast to NRT1.1-mRNA the NRT1.1-protein levels are increased in LR primordia of nitrate starved roots with a concomitant decrease of

Figure 1



Schematic phenotypes of *Arabidopsis thaliana* Col-0 plants in single-nutrient deficiency. Representative phenotypes are shown for plants grown on vertical agar plates with media lacking the specified nutrient (except for nitrate which was supplied at low level), based on published data [1•,2•]. Phenotypes in nutrient-sufficient media and phenotypes reported for localized nitrate treatment [3] are shown for comparison. Length of primary and lateral roots is represented by the length of the grey spheres, and lateral root density is represented by their width. Green ovals represent shoot biomass.