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Nitrogen signalling pathways shaping root system architecture: an update

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Root system architecture is a fundamentally important trait for resource acquisition in both ecological and agronomic contexts. Because of the plasticity of root development and the almost infinite complexity of the soil, root system architecture is shaped by environmental factors to a much greater degree than shoot architecture. In attempting to understand how roots sense and respond to environmental cues, the striking effects of nitrate and other forms of nitrogen on root growth and branching have received particular attention. This minireview focuses on the latest advances in our understanding of the diverse nitrogen signalling pathways that are now known to act at multiple stages in the process of lateral root development, as well as on primary root growth.

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Introduction

How efficiently plants explore the soil for their essential supplies of water and nutrients is largely determined by the architecture of their root systems [1]. Root development has long been known to be highly plastic and subject to modification by a wide range of environmental factors [2], amongst the most intensively studied of which is the availability and distribution of different forms of environmental N [3]. Plant roots can absorb and assimilate N in a variety of different forms, both inorganic (nitrate and ammonium) and organic (amino acids and peptides) [4] and the intrinsic complexity and heterogeneity of soils means that there are huge variations in the concentration and distribution of these [5–7].

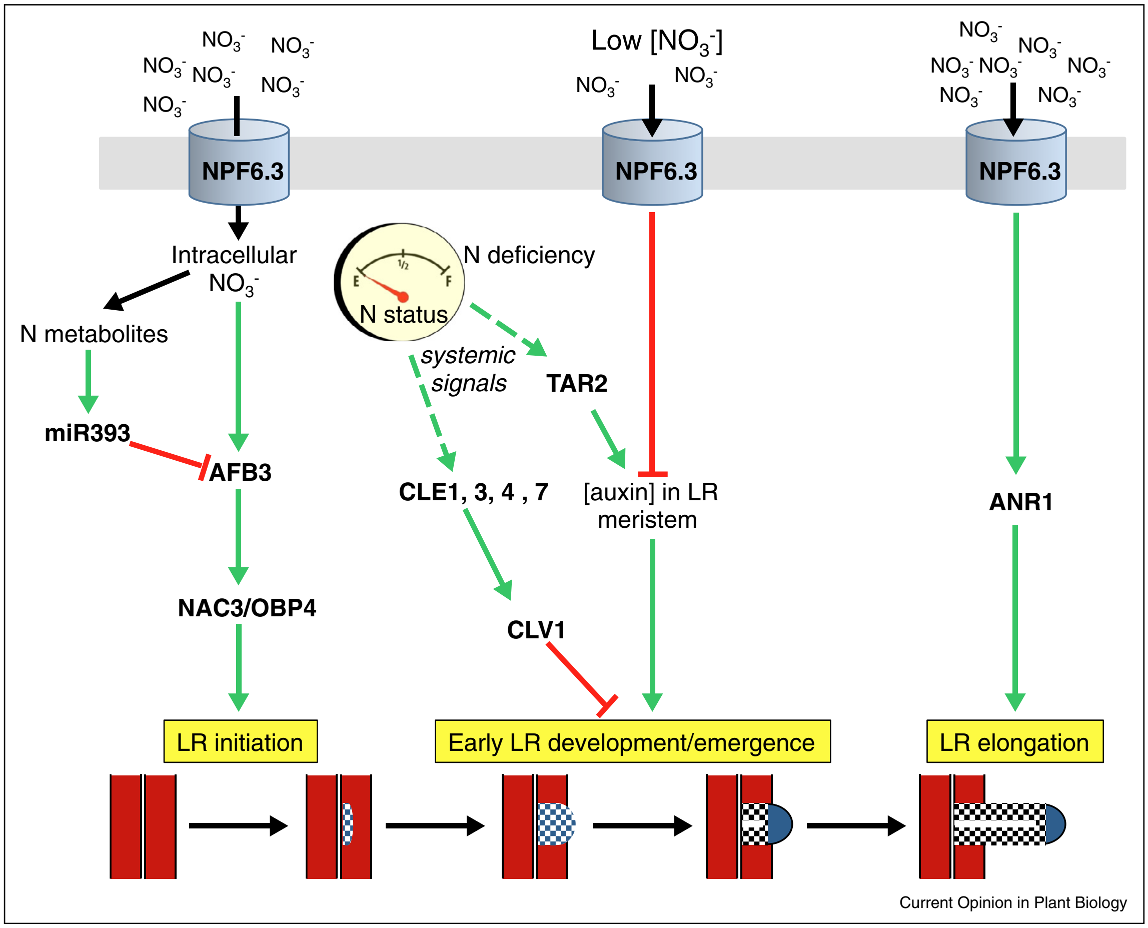
In terms of developmental plasticity, it is generally observed that lateral roots (LRs) are more sensitive to variations in the N supply (and other environmental signals) than are primary roots [8]. The post-embryonic and multistage nature of LR development provides multiple checkpoints at which root branching can be (and is) regulated: LR development begins with initiation of founder cells in the root pericycle just behind the primary root apex, continues with the formation of a cluster of cells that constitutes the LR primordium and is followed by the formation of a radially symmetrical meristem [9]. In Arabidopsis, activation of this meristem to produce a mature elongating LR only occurs after the LR has emerged from the primary root [9]. Even after activation of the meristem, the elongation rate of the LR may be regulated both by the local external conditions [10] and by endogenous factors [11]. Although the primary root is less sensitive than LRs to the N supply, there are cases where significant effects of nitrate [12,13•,14] or amino acids [15,16] on primary root growth have been observed and the nature of the regulatory mechanisms investigated.

This short review will focus on advances in the past two years in our understanding of the signal transduction pathways that shape root architecture in response to variations in the external N supply and the plant's N status. For in-depth background information the reader is referred to a series of comprehensive reviews on this and related topics that have appeared in recent years [15,17–22]. Also of relevance are recent reviews on nitrate signalling in the context of the regulation of gene expression [21,23,24]. The signalling pathways discussed here are depicted schematically in Figures 1 and 2.

Stimulation of lateral root elongation by external nitrate

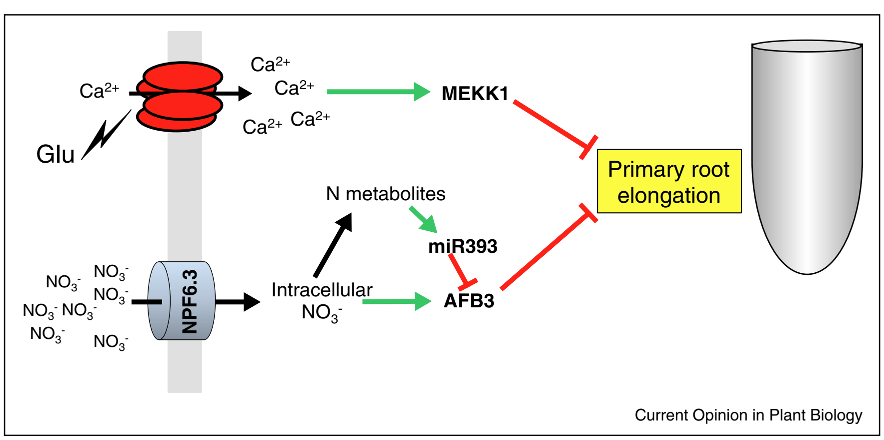
Early studies of the effect of nitrate on root branching in Arabidopsis were concerned with the ability of a localised nitrate treatment to stimulate LR elongation [25,26], the classic foraging-type response described in the 1970s by Drew and colleagues with barley [27]. Experimentally, the value of using a localised rather than a uniform nitrate treatment is that it allows the specific effect of external nitrate on LR growth to be studied under conditions where systemic effects due to changes in the N status of the plant can be largely discounted [10,25]. Using this approach, the positive effect of a localised nitrate treatment on LR proliferation in Arabidopsis was found to depend primarily on exposure of mature elongating LR tips to the elevated nitrate concentration [25,28]. A signalling pathway that

Figure 1



Multiple pathways regulating the LR response to the N supply in Arabidopsis. Only those pathways discussed in the present review are depicted. Black arrows indicate nitrate transport or assimilatory pathways, green arrows indicate positive signalling steps and red lines indicate negative signalling steps, broken lines indicate systemic signals. See text for further explanation.

Figure 2



Regulation of primary root growth in Arabidopsis by external nitrogen. The receptor for the external glutamate signal is shown as a glutamate-gated Ca^{2+} channel because these are known to be active in root tips [32•], but their specific role in this pathway is unconfirmed. Note that nitrate has also been reported to have a stimulatory effect on primary root growth both indirectly, by antagonising the inhibitory effect of glutamate, and directly, via an unknown pathway [14]. See text for further information.