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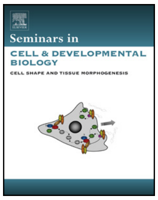

Review

Understanding nitrate uptake, signaling and remobilisation for improving plant nitrogen use efficiency

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ABSTRACT

The majority of terrestrial plants use nitrate as their main source of nitrogen. Nitrate also acts as an important signalling molecule in vital physiological processes required for optimum plant growth and development. Improving nitrate uptake and transport, through activation by nitrate sensing, signalling and regulatory processes, would enhance plant growth, resulting in improved crop yields. The increased remobilisation of nitrate, and assimilated nitrogenous compounds, from source to sink tissues further ensures higher yields and quality. An updated knowledge of various transporters, genes, activators, and microRNAs, involved in nitrate uptake, transport, remobilisation, and nitrate-mediated root growth, is presented. An enhanced understanding of these components will allow for their orchestrated fine tuning in efforts to improving nitrogen use efficiency in plants.

Contents

1. Introduction

Nitrogen (N) is the second most important input factor, after water, for crop production, worldwide. In the recent past, most crop varieties were selected and bred under optimum N conditions, hence they thrive better under higher N supply. Concurrently, since large-scale synthetic N fertilizer production became prevalent, N has become an affordable input by most farmers, resulting in the increased usage of N fertilizers as an assurance for higher crop yields. The application of N fertilizer has increased over 8-fold since 1961, with an annual use of approximate 108 million tonnes for agricultural production worldwide in 2013 [1]. Unfortunately, the applied N fertilizer is not used efficiently, with, on average, less than 40% of the applied N being taken up by cereals such as wheat, maize, rice, barley and sorghum [2–4]. The remaining N is lost to the environment through processes including gaseous losses as volatilization, leaching, surface runoff and microbial consumption [3]. Therefore, the excessive use of N fertilizers increases the cost of crop production, as well as causing environmental pollution. Hence, crop varieties which sustain growth and yield under low N conditions would benefit for economic and environment savings.

Among the different forms of N, nitrate (NO_3^-) is the main source in the majority of agricultural soils, and is preferentially taken up by most cereals except for paddy rice where ammonium (NH_4^+) form is ideal [4,5]. Nitrate is often limited in availability in most agricultural soils, with significant temporal and spatial fluctuations. As sessile organisms, plants therefore need to be able to rapidly adapt to these variable soil nitrate concentrations to

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optimize N capture. In order to enhance the ability of plants to capture the applied N fertilizer, it is important to understand the processes by which plants acquire nitrate and how this process is regulated [6,7]. Most plants have two types of nitrate uptake systems, with associated transporter genes; the Low Affinity Transport System (LATS) when nitrate availability is >0.5 mM and the High Affinity Transport System (HATS) when the external nitrate availability is <0.5 mM [6]. Once nitrate is taken up into the plant, it is assimilated into amino acids in a series of reactions facilitated by a well-known suite of enzymes, although when nitrate is sufficiently available it can be temporarily stored in vacuoles before assimilation. Nitrogenous compounds formed during assimilation are stored in source tissues (e.g. leaves in cereals) during vegetative growth, then remobilised to sinks (e.g. developing grains in cereals) during reproductive phase, in a process known as N remobilization. Efficient remobilization of a plant's nitrogenous compounds during senescence is an important contributor to large and high quality yields, otherwise N entities can remain tied-up and lost in dead source tissues.

Apart from its role as a nutrient element, nitrate acts as an important signalling molecule in processes, such as inducing the expression of genes involved in its own transport and assimilation [8], lateral root development [9], leaf development [10], and flowering time [11]. The mechanisms, genes and enzymes involved in nitrate assimilation are well studied and defined; whereas our knowledge of nitrate sensing and signalling processes, the underlying control for nitrate transporters, and the regulation of N remobilization is still not complete, instead being constantly updated with new research findings. This review highlights different aspects of the nitrate response, including its uptake, sensing, signalling and remobilisation, as well as the key activators and regulators underlying these processes that can contribute to our efforts for improving nitrogen use efficiency (NUE) in crop plants.

2. Nitrate uptake and transport

Four families of transporters are known to contribute to nitrate uptake and transport in plants; the Nitrate Transporter 1/Peptide Transporter (NPF) family [12], the Nitrate Transporter 2 (NRT2) family, the Chloride Channel (CLC) family, and Slow Anion Associated Channel Homolog (SLC/SLAH) family [13,14]. Transporters of NPF and NRT2 families are mainly involved in nitrate uptake from soil/external media, their localisation in plants is shown in Fig. 1 and function discussed in brief here. In this review, the genes/proteins without a prefix are from plant species Arabidopsis.

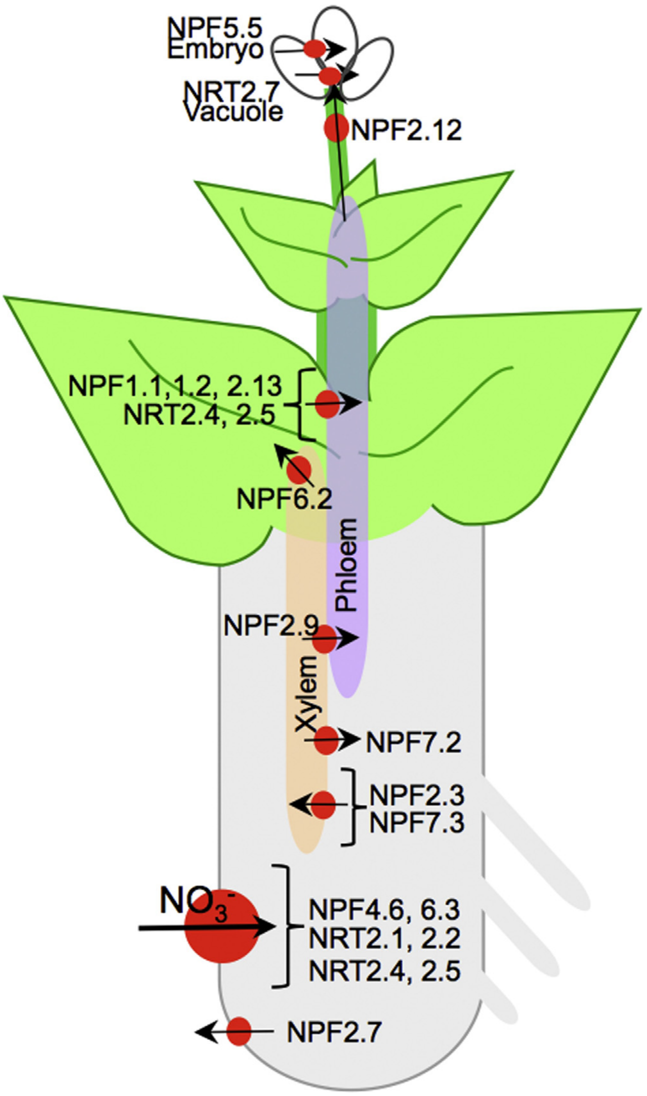

Fig. 1. Nitrate transporters and their localisation in plant. Transporters from NPF and NRT2 families are shown with their role in nitrate update in roots (NPF4.6, 6.3, NRT2.1, 2.2, 2.4, 2.5) from external media and efflux (NPF2.7), nitrate loading (NPF2.3, 7.3) and unloading (NPF7.2) from root-to-xylem and xylem-to-phloem (NPF2.9), nitrate loading from older leaf to phloem (NPF1.1,1.2, 2.13, NRT2.4, 2.5) for nitrate relocation to younger leaves, nitrate translocation to seed (NPF2.12), nitrate translocation within seed to embryo (NPF5.5) and vacuole (NRT2.7).

The NPF family (formerly the NRT1/PTR family) comprises of 53 known genes in Arabidopsis, and up to 139 genes in higher plants, divided in to eight subfamilies [13,14]. Transporters in this gene family generally have a low-affinity for nitrate, with the exception of NPF6.3 (CHL1/NRT1.1) which has a dual high- and low-affinity for nitrate, depending on the phosphorylation state of the T101 residue [15]. NPF6.3 is expressed in several tissues; root, young leaves and flower buds, where it acts in nitrate uptake from external media, as well as nitrate translocation in aerial organs [9,14,16]. NPF6.3 homologous genes have been identified in cereal crops. For instance, co-orthologous genes in wheat TaNPF6.1, TaNPF6.2, TaNPF6.3, and TaNPF6.4 and in rice, OsNPF6.3, OsNPF6.5 (OsNRT1.1b), and OsNPF6.4 with their distinctive expression patterns in roots or shoots [17–19]. OsNPF6.5 (OsNRT1.1b) has been characterised for root nitrate uptake [19]. NPF4.6 (NRT1.2/AIT1) and NPF2.7 (NAXT1) are other two members of NPF family currently known to be involved in root nitrate uptake. NPF4.6 is constitutively active in root tip where it acts in nitrate influx, [20], whereas NPF2.7 is mainly involved in nitrate efflux to external media [21]. All other characterised NPFs are mainly associated with the internal transport of nitrate in processes such as, xylem and phloem loading, and translocation to leaves or seed (Fig. 1).

NRT2 gene family members are high-affinity nitrate transporters, with only eight NRT2 transporter identified in plants [22]. Seven NRT2 transporters have been characterised in Arabidopsis [23], with four of these, NRT2.1, NRT2.2, NRT2.4, and NRT2.5, known to be involved in root nitrate influx. NRT2.1 is the main nitrate inducible component of the HATS, which is briefly expressed under nitrate starvation, and repressed at high nitrate levels [24,25]. In wheat, TaNRT2.1 was reported to have a putative major role in nitrate uptake especially during post-flowering [26]. NRT2.4 has been shown to play a major role in nitrate acquisition under very low external nitrate concentrations. NRT2.5 plays a similar role to NRT2.4, with both expressed in the shoots, contributing to nitrate loading in the phloem [27,28]. NRT2.2 on the other hand, with its low expression, has a minor role in nitrate uptake [24,25]. To function in their nitrate uptake capacity, interaction of NRT2

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