IN BRIEF

A Nitrate Transporter for Both Roots and Shoots

Nitrogen availability is often a limiting factor in plant growth and crop productivity, but the application of nitrogen fertilizers to counteract nitrogen deficiencies can have detrimental economic and environmental effects. Therefore, it is important to understand mechanisms of nitrogen uptake, transport, and utilization within the plant. The most common form in which nitrogen is assimilated by the plant is nitrate (NO$_3^-$), and plants have evolved a variety of nitrate transporters with different localizations and functions: uptake of nitrate by roots, transport in the xylem or phloem, regulation of nitrate content in seeds, and transport into the vacuole for storage (Dechorgnat et al., 2011).

*Arabidopsis thaliana* NRT2.1 is a prominent high-affinity nitrate transporter that functions at low external nitrate concentrations and plays an additional role in lateral root initiation that is independent of this transport function (Little et al., 2005). *Kiba et al.* (pages 245–258) present an extensive characterization of the less well known NRT2.4 and show that it is a high-affinity nitrate transporter important in both root uptake and phloem loading and that its spatial and temporal expression complements that of NRT2.1. They show a complementary two-step response to nitrogen deficiency regarding nitrate concentration and spatial expression in the root, a finding that represents significant progress in the nitrate transport field.

In nitrate-containing media, NRT2.4 expression was detected at low levels in roots and was undetectable in shoots, but after 3 d of nitrogen starvation was induced 12-fold in roots and became detectable in shoots. By contrast, NRT2.1 expression was high in roots in the presence of external nitrate and, after a transient increase, was relatively unchanged after 3 d of nitrogen starvation. In hydroponically grown plants, nitrogen starvation for 10 d resulted in a dramatic increase in NRT2.4 expression, and nitrate addition reduced subsequent expression by >90%. NRT2.1 expression showed a markedly different pattern, suggesting that these two transporters have complementary roles in nitrogen acquisition in the plant.

NRT2.4 expression was undetectable in nitrogen-replete conditions and was expressed during nitrogen starvation but mainly in lateral roots and younger parts of the primary root. This was in marked contrast with NRT2.1, which was expressed chiefly in the older part of the primary root regardless of nitrogen status. More specifically, the authors localized NRT2.4 expression to lateral root epidermal cells (see figure). NRT2.4 expression in shoots of these plants was limited to the primary veins of leaves and inflorescences and was adjacent to the phloem parenchyma.

The authors also expressed the NRT2.4 cDNA in the *nrt2.1-1* mutant, which is deficient in high-affinity nitrate uptake, and measured uptake of $^{15}$N nitrate in hydroponic conditions. NRT2.4 overexpression correlated with increased nitrate influx, increased nitrate content in shoots, and increased biomass. The ability of NRT2.4 to transport nitrate was confirmed by heterologous expression of NRT2.4 in *Xenopus laevis* oocytes.

The authors then used *nrt2.4* mutants alone or in combination with other *nrt2* mutants to show that NRT2.4 functions in the very-high-affinity range for nitrate uptake, promotes growth and nitrate influx at low external nitrate, and is required to maintain nitrogen levels in leaf exudates. In conclusion, they discuss the relationship of NRT2.4 relative to other nitrate transporters and propose roles for NRT2.4 in both high-affinity nitrate uptake in roots and phloem-related transport in shoots. As a result of this work, we now have a more complete picture of how the functions of distinct nitrate transporters are integrated at the whole-plant level.

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REFERENCES


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NRT2.4 is expressed primarily in the epidermis of lateral roots. NRT2.4$_{ng}$β-glucuronidase staining patterns are shown in roots of an intact seedling (A) and in a cross section of a lateral root (B). Bars = 1 cm for (A) and 10 μm for (B). (Reprinted from Figure 3 of Kiba et al. [2011].)
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