Control of Nitrate Uptake/Assimilation and Plant Productivity

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Abstract

Nitrogen is one of the major elements that limit plant growth and productivity in both natural environments and plowed fields. To increase the harvest yield, nitrogen fertilizers are widely used in agriculture. The form of nitrogen commonly used as fertilizer is ammonium (NH_4^+), but in temperate aerobic soils, ammonium is rapidly oxidized to nitrate (NO_3^-) by nitrification. The resulting nitrate hence serves as the major source of nitrogen for most cultivated plants. Nitrate is, however, known to cause environmental and health problems. This paper summarizes current knowledge about the critical steps that determine the nitrate flow in plants and discusses possible strategies for improving the nitrate use efficiency.

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Problems caused by nitrate in the environment and in the plant body

Although plants have active transporters for nitrate uptake, large amounts of nitrate are lost from the soil by leaching, resulting in increased nitrate concentrations in both the surface and underground water. Accumulation of nitrate in lakes and ponds leads to bloom of cyanobacteria (known as “aoko” in Japan). Nitrate in drinking water would cause health problems such as “blue baby syndrome,” and carcinogenesis when it is converted to nitrite (NO_2^-) in the human body. When taken up by plants, on the other hand, nitrate is reduced to ammonium via nitrite, and the ammonium is fixed as the amide nitrogen of glutamine. The amide nitrogen of glutamine is subsequently transferred to various organic compounds to form a variety of nitrogenous compounds essential for plant growth. It should be noted, however, that the plants accumulate high concentrations of nitrate (i.e., >150 mM) in the vacuole and do not assimilate all the nitrate they have absorbed from the soil. When used as food, nitrate in the plant body can cause health problems as described above. It is therefore desirable to prevent nitrate accumulation in the plant body. It is also important to improve the overall efficiency of nitrate assimilation so that the use of nitrogen fertilizer can be minimized.

Regulation of expression of the nitrate transporter genes

One of the possible strategies for reducing the intracellular nitrate is to modify the regulation of expression of the nitrate transporter genes in roots. Similar to other organisms capable of nitrate assimilation (i.e., certain bacteria, cyanobacteria, green algae, and fungi), higher plants seem to have two distinct mechanisms for regulation of the genes involved in nitrate assimilation. One of these is the “global nitrogen regulation”, which represses or downregulates expression of the genes involved in nitrogen acquisition when cells have sufficient amounts of fixed nitrogen. The other is the “substrate induction”, which involves the substrate of nitrate assimilation, i.e., nitrate (or nitrite), as the activator of expression of the relevant genes. Unlike in the other organisms capable of nitrate assimilation, the “substrate induction” seems to override the negative feedback by the “global nitrogen regulation” in higher plants. As a result, plant cells express the nitrate assimilation genes even when the plant is in nitrogen-replete conditions, if nitrate is present in the soil. This seems to cause continued uptake of nitrate into the cell, resulting in accumulation of excess nitrate in the plant body. Modification of the cis-acting regulatory elements involved in the substrate induction of the nitrate transporter genes may lead to specific decline in the expression level of the nitrate transporter genes and thereby reduce the intracellular nitrate level in the plant cell.

Control of relative contribution of roots and shoots in nitrate assimilation

Another possible means to lower the nitrate levels, specifically in leaves, is to modify the relative contribution of the roots and shoot in nitrate assimilation. The relative contribution of roots and shoots is variable among different species of plants; in some plants, the contribution of roots in nitrate assimilation is small and most of the nitrate is transported to the shoot. In certain plant species, on the other hand, nitrate is assimilated mostly in the root, and the fixed nitrogen is transported to the shoot as amino acids. It is therefore, theoretically possible to genetically engineer a plant that assimilates nitrate entirely in the root. To achieve this type of metabolic engineering, we need to control the expression levels of the enzymes involved in nitrate assimilation and also of the enzymes involved in supply of carbon skeletons and metabolic energy for nitrogen assimilation. Since the root cells are dependent on the supply of carbon and energy from the leaf cells, understanding of the metabolic interactions between the shoot and root is also necessary.

Importance of basic research for genetic modification of nitrate assimilation in plants

As has been discussed above, currently available information about nitrate assimilation in plants allows us to design some strategies for improvement of the nitrate use efficiency in plants. However, to actually construct a genetically modified plant, more detailed information about the regulation of the relevant genes is necessary; the molecular mechanism(s) regulating the nitrate transporter genes needs to be fully understood. The molecular basis for the different contribution of roots in nitrate assimilation in different plant species also needs to be elucidated. Thus, the importance of basic research on the nitrate assimilation pathway cannot be overemphasized.