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Review

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Ammonium homeostasis and signaling in plant cells

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Abstract Nitrogen is an essential macronutrient in plant growth and development. Ammonium is one of the major inorganic nitrogen forms for root uptake. The homeostasis of ammonium in the plant cell is under tight control to prevent ammonium toxicity when in excess. In the ammonium signaling pathway, internal and external ammonium can be detected by specific sensors, which in turn triggers a series of proper plant ammonium responses including transcription regulation and phosphorylation. Ammonium absorption is mainly mediated by the root-located ammonium transporters, which are key regulators in the nitrogen signaling pathway. Many researchers have attempted to unravel the mechanisms of ammonium uptake by the transporters. Fine-tuned modulation of ammonium homeostasis is necessary to maintain an appropriate level of ammonium in the cytoplasm, which is a balance of ammonium efflux, assimilation and compartmentation. Recently, there has been important progress in revealing the ammonium sensing and signaling mechanisms. In this review, we focus on the homeostatic regulation and signaling of cytosolic ammonium.

Keywords Ammonium · Homeostasis · Ammonium signaling

1 Introduction

Nitrogen is one of the most abundant elements and is essential for plant growth and development; about 70 % of all ions acquired by plants contain nitrogen [1]. Ammonium (used hereafter without distinguish between gas and ammonium ions) is a preferential reduced nitrogen source for many microorganism and plants [2]. Nitrogen deficiencies occur in almost all habitats at least during one or several phases of growth, which results in reduced growth, lowered crop yield and quality. Therefore, nitrogen fertilizers have been used intensively in agriculture, which results in increased ammonium accumulation in the soil and in many other natural ecosystems [3].

In the cell, ammonium is derived from either direct uptake by ammonium transporters from the soil or from NO_3^- reduction in root [4]. It is also produced during photorespiration or amino acid catabolism. Moreover, excess ammonium will inhibit plant growth or generate toxicity to plants; therefore, concentration of ammonium in the plant cell must be tightly controlled [5, 6]. Due to fluctuations in availability, the uptake for ammonium needs to be fine-tuned in order to allow optimal growth of plants and to prevent accumulation of ammonium up to toxic levels. Thus, plant cells have evolved elaborate systems both for sensing the changes of internal and external ammonium level, as well as for acquiring adequate amounts of ammonium from the environment and transporting it throughout the body. Recently, there has been important progress in revealing the ammonium sensing and signaling mechanisms. This review focuses on recent developments in ammonium homeostasis regulation and signaling in higher plants.

2 Ammonium response and toxicity

Ammonium is the major nitrogen source, and it is essential for plant growth. Improving the use of ammonium is the

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key to improve agricultural production. It has been reported that ammonium regulates lateral root development in an ammonium transporter1;3 (AMT1;3)-dependent manner [7]. However, aside from its advantageous effects, the downside of ammonium is the well-known phenomenon of toxicity when in excess. The increasing application of N fertilizers has led to ammonium toxicity in crops. Most plants display toxic symptoms when external ammonium supplies are high. Typical responses of ammonium toxicity are reduction in root-to-shoot ratio, inhibition of seed germination and seedling growth, and increase in lateral root number [6]. In sensitive species, ammonium toxicity can result in 15 %–60 % drop in yield or even death [6].

Although the exact mechanism underlying ammonium toxicity is still unclear, several hypotheses have been proposed to explain why ammonium is toxic to plants [3, 6, 8]. Several reports have postulated that acidification of external environment of root [9] and/or intracellular pH disturbance [10] may be the main factors leading to toxicity symptoms in plants. This is because NH_4^+ uptake mechanisms are coupled to H^+ extrusion into the rooting medium and H^+ release is also associated with NH_4^+ incorporation into protein [11]. On the other hand, internal pH could be increased by NH_4^+, which influences cell growth. For example, the root hair cells treated with pH7, 10 mmol/L NH_4Cl were depolarized by alkalinizing the cytoplast 0.3–0.5 U, and as a result, root hair growth was inhibited [12].

Another mechanism underlying ammonium toxicity is the high energy demand in pumping ammonium out of the cells. This finding is based on the studies of an ammonium-sensitive and an ammonium-tolerant domesticated species (barley and rice, respectively). Barley (*Hordeum vulgare*) and rice (*Oryza sativa*) have been used for comparing NH_4^+ fluxes and energetics in NH_4^+ acquisition. Barley, as an ammonium-sensitive species, is susceptible to ammonium toxicity. It is reported that almost 80 % of the primary influx are pumped out of the root cell [3]. High energy is needed to fuel this futile ion cycling, with respiration in the root increased by 40 % [13]. Under high level of ammonium, the efflux is higher in barley than in rice, occupying 76 % and 53 % of the influx for barley and rice separately [8]. As external ammonium levels increase, this futile cycling increases as well, underlying barley's sensitivity to ammonium toxicity.

Relative lower levels of ammonium are accumulated in rice, which is why rice is known for its high tolerance for ammonium. It has been proposed that the electronic potential across the rice root cell plasma membrane is reduced under conditions of elevated external ammonium, and this depolarization of the cell results in relatively lower amounts of ammonium accumulating in rice, which is one of the reasons for the higher tolerance against ammonium toxicity in rice [3]. However, this mechanism has not been observed in barley, and the high energy lost in pumping out excess ammonium to keep the membrane potential suggests the potential difference is insensitive to high external levels of ammonium.

3 Ammonium homeostasis: uptake, assimilation and compartmentation

3.1 Ammonium uptake

As mentioned above, plants absorb nitrogen directly from the soil. Many factors can influence ammonium uptake, such as internal and external ammonium levels, external pH, light and endogenous N assimilates [14]. Tight control of uptake is one of the efficient methods in adjusting cellular ammonium levels. Ammonium uptake systems have been extensively studied.

Ammonium transport (Amt) proteins shuttle ammonium across the plant membranes specifically. Two broad categories of ammonium transporter systems have been identified in plant roots. HATS, the high-affinity transport systems, contribute to ammonium uptake in the low external concentration range (0.5–1 mmol/L), and low-affinity transport systems (LATS) predominantly operate at higher external concentrations (>1 mmol/L) [15].

In plants, high-affinity uptake of ammonium is mediated by ammonium transporter/methylamine permease/rhesus (AMT/MEP/Rh) superfamily [16, 17]. Six members of the AMT family in *Arabidopsis thaliana* have been found, which fall into two clades, AMT1 and AMT2. Among these, AMT1;4 is expressed in pollen, mediating pollen nitrogen supply, while the other five members are all expressed in root [18, 19]. AMT1;1, AMT1;3 and AMT1;5 are located in outer root cells or root hairs and possess the highest ammonium affinities for absorbing ammonium from the soil. AMT2;1 is expressed more highly in shoots than in roots and is most likely to play a role in ammonium retrieval in roots and leaves [20, 21]. Increasing evidence shows that root AMT transporters are responsible for major uptake of ammonium. Under N-limiting conditions, transcript levels of *AMT* in *Arabidopsis* roots clearly increase [16]. Constitutively expressed *OsAMT1;1* is a nitrogen-responsive gene, and it encodes a plasma membrane protein. *OsAMT1;1* overexpression plants enhanced permeability of ammonium and showed superior growth under optimal and suboptimal ammonium conditions [22].

The regulation of ammonium on AMT transporters is also reflected in the posttranscriptional level. The highly conserved C-terminal domain of AMT/MEP is necessary for allosteric regulation [23, 24]. Ammonium-triggered