



## Review article

# Review: Mechanisms of ammonium toxicity and the quest for tolerance



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## ABSTRACT

Ammonium sensitivity of plants is a worldwide problem, constraining crop production. Prolonged application of ammonium as the sole nitrogen source may result in physiological and morphological disorders that lead to decreased plant growth and toxicity. The main causes of ammonium toxicity/tolerance described until now include high ammonium assimilation by plants and/or low sensitivity to external pH acidification. The various ammonium transport-related components, especially the non-electrogenic influx of  $\text{NH}_3$  (related to the depletion of  $^{15}\text{N}$ ) and the electrogenic influx of  $\text{NH}_4^+$ , may contribute to ammonium accumulation, and therefore to  $\text{NH}_3$  toxicity. However, this accumulation may be influenced by increasing  $\text{K}^+$  concentration in the root medium. Recently, new insights have been provided by “omics” studies, leading to a suggested involvement of GDP mannose-pyrophosphorylase in the response pathways of  $\text{NH}_4^+$  stress. In this review, we highlight the cross-talk signaling between nitrate, auxins and  $\text{NO}$ , and the importance of the connection of the plants’ urea cycle to metabolism of polyamines. Overall, the tolerance and amelioration of ammonium toxicity are outlined to improve the yield of ammonium-grown plants. This review identifies future directions of research, focusing on the putative importance of aquaporins in ammonium influx, and on genes involved in ammonium sensitivity and tolerance.

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## 1. Nitrogen: a global issue with socio-economic and environmental consequences

We live in a world surrounded by nitrogen ( $\text{N}_2$ ): 78% of the Earth’s atmosphere is  $\text{N}_2$ . However, to be available to plants,  $\text{N}_2$  must first be converted into reactive nitrogen, a term which encompasses all N forms that are not involved in C–N bonding and elemental  $\text{N}_2$ , and applies to species including  $\text{NH}_3$  to  $\text{NO}_3^-$ , cov-

Abbreviation: AQP, aquaporins; AMT, ammonium transporters; CPS, carbamoyl phosphate synthase; NSCC, non-specific cation channel; NUE, nitrogen use efficiency; OEC, oxygen-evolving complex; ROS, reactive oxygen species.

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ering the valence spectrum from  $-3$  to  $+5$  (excluding  $0$ , the valence of  $N_2$ ). In nature, the conversion of  $N_2$  into reactive nitrogen is mediated by biological  $N_2$  fixation and by atmospheric lightning. However, the fixation of  $N_2$  through natural processes is insufficient to ensure the food production necessary to maintain the current and future human population. Agriculture requires the intensive use of N fertilizers: nitrate ( $NO_3^-$ ), ammonium ( $NH_4^+$ ) and/or urea ( $CH_4N_2O$ ). Due to crop breeding for high yields irrespective of the amounts of fertilizer required, most current crops exhibit very low nutrient (including N) use efficiency. The intensive application of  $NO_3^-$ - and  $NH_4^+$ -based fertilizers causes environmental problems, including the eutrophication of water reservoirs, aquifer contamination, and atmospheric pollution; these problems are recognized as a serious worldwide issue of public and economic concern. A recent economic analysis indicated that excess reactive nitrogen in the environment and its contributions to climate change and biodiversity loss cost the European Union between 70 and 320 billion € per year [1]. The scientific proposal “20:20 for 2020 goal” addressed global intergovernmental cooperation to improve N Use Efficiency (NUE), and was intended to provide environmental and health benefits worth approximately 160 (50–370) billion € per year [1]. The aim of the “20:20 for 2020 goal” is to improve NUE by 20%, thus reducing the use of N by 20 million t/year by 2020 [1]. Understanding the mechanisms underlying N use by plants and improving its use efficiency is therefore of social, economic, agricultural and ecological importance.

Soil  $NO_3^-$  and  $NH_4^+$  concentrations are usually unpredictable and change with time and location. The abundance of  $NH_4^+$  in ecosystems is determined by many factors, including the chemical nature of the soil, pH, temperature, the accumulation of organic compounds, oxygenation, light, and  $CO_2$  [2–4]. Soils with low pH and anoxic conditions (such as those found in wetlands including fens, bogs, saltmarshes, mangroves and rice paddies) exhibit higher ammonification than nitrification rates [2,5] and so are rich in  $NH_4^+$ . In many soils of natural and semi-natural ecosystems,  $NH_4^+$  is the predominant N source, presenting a mean concentration of 2 mM in boreal and temperate forest soils [6]. Plant growth in these ecosystems is mainly supported by direct (via roots) or indirect (via mycorrhizae)  $NH_4^+$  uptake. At low concentrations ( $<3$  mM),  $NH_4^+$  is typically the N source preferred by plants, but above a certain threshold,  $NH_4^+$  becomes toxic [7]. This threshold depends on plant species and on variety (in crops) (as examples, see [8–11]). Environmental factors such as temperature, soil pH,  $CO_2$  concentration and light intensity can affect the threshold for  $NH_4^+$  toxicity (e.g., [3,4,7,12]; Fig. 1). Crops, such as potato or sugar beet, are generally more sensitive to  $NH_4^+$  than their respective wild relatives (reviewed in [2]). However, some crops, such as rice, blueberries and onions, are adapted to high  $NH_4^+$  concentrations [2] and rarely reach the threshold for  $NH_4^+$  toxicity. In the case of trees, higher sensitivity to ammonium is often found in early-successional trees, such as poplars or douglas-fir, rather than in late-successional conifers such as spruce species [2].  $NH_4^+$  sensitivity is not unique to terrestrial plants, but has also been observed in animals, (including mammals) [13], algae [14], cyanobacteria [14,15] and yeast [16], among others.

Although understanding of the causes of  $NH_4^+$  sensitivity/tolerance has greatly improved during the last two decades, the plant traits that are responsible for plant  $NH_4^+$  sensitivity or tolerance remain unclear. This review highlights key factors that determine plant tolerance or sensitivity to  $NH_4^+$  nutrition, especially in crops, and draws comparisons with nitrate where useful. The review also summarizes and integrates recent research addressing: (i) the main causes of  $NH_4^+$  toxicity in plants and (ii) how these causes can be targeted to achieve plant tolerance to  $NH_4^+$  nutrition.

## 2. Ammonium toxicity in plants: from classical to recent hypothesis

$NH_4^+$  toxicity in plants is not a new topic; the detrimental visual effects of  $NH_4^+$  nutrition on roots, leaves and plant growth were first reported more than a century ago (e.g., [17]). Since then, much work has been conducted to elucidate the mechanisms underlying the toxicity of  $NH_4^+$  nutrition.

### 2.1. Classical hypothesis of plant ammonium toxicity

$NH_4^+$  toxicity symptoms include: reduced plant growth, changes in root architecture, decreases in the root/shoot ratio, and leaf chlorosis, among others [7,18]. These phenotypic symptoms reflect the integrated effect of  $NH_4^+$  excess, which causes the following: inhibition of cations ( $K^+$ ,  $Mg^{2+}$  or  $Ca^{2+}$ ) uptake and consequent changes in plant ion balance; intra-cellular alkalization and extracellular acidification; the inhibition of root respiration and stimulation of photorespiration; interference with photosynthetic activity; the altered expression/activity of  $NH_4^+$  assimilating enzymes; the disruption of hormonal homeostasis; increased oxidative stress; and high energy cost to maintain low levels of cytosolic  $NH_4^+$  content (e.g., [7,9,12,18–20] and references cited therein) (Fig. 1).

To avoid toxicity, plants need to maintain a fine balance between the uptake, production, and consumption of  $NH_4^+$  [18]. This leads to the question of the nature of plants' first response to high levels of  $NH_4^+$ . In  $NH_4^+$ -sensitive plants, such as *Arabidopsis* sp., shoots tend to be the most sensitive part of the plant to  $NH_4^+$  nutrition [21]. However, roots constitute the first  $NH_4^+$  sensor, and the initial signals of  $NH_4^+$  toxicity appear at root level with a severe modification of the root system architecture; commonly observed modifications include: shorter primary root systems [e.g. [8,22]]; the inhibition of root elongation, embracing primary and lateral roots [22–24]; the stimulation of lateral root branching [22,24], with changes in the insertion of lateral roots in the main root [24]; and a loss of gravitropism [26]. It is necessary to understand whether these effects are part of a cascade-type response or merely the summation of several simultaneous plant responses to the presence of  $NH_4^+$  (or to one product of its metabolism). Studies of *Lotus japonicus* using split-root systems showed that root-specific  $NH_4^+$ -induced responses are mediated by  $NH_4^+$  transporters [23,25] and are more related to the perception of  $NH_4^+$  than to its assimilation. A member of the *L. japonicus* AMT1-type transporter family (*LjAMT1;3* gene) appears a good candidate for the agent responsible for promotion of the characteristic  $NH_4^+$ -root phenotype for the following reasons: its transcription is induced in the same range of  $NH_4^+$  concentrations that promotes the appearance of the  $NH_4^+$ -root phenotype; and its overexpression is sufficient for phenocopying the short-root phenotype into transgenic plants [23]. The function of AMT1;3 as a mediator of the short-root phenotype induced by  $NH_4^+$  nutrition was also observed in *Arabidopsis* [25]. Together, these observations suggest that  $NH_4^+$  is locally sensed, and that it is possible that the  $NH_4^+$ -sensing machinery employs regulatory modules similar to those that have been suggested to play a role in nitrate sensing.

Exogenous  $NH_4^+$  (in the root medium) only reaches plant leaves after saturating the storage capacity of the root system. In leaves, the toxic effects described are controversial and are mainly related to the effect of  $NH_4^+$  on photosynthesis and its capacity to generate oxidative stress.  $NH_4^+$  (1 mM) was described as uncoupling photophosphorylation in isolated spinach (*Spinacia oleracea*) thylakoids in the late 1950s [27]. Forty years later, the uncoupling effect of  $NH_4^+$  was ruled out, based on a study performed on bean (*Phaseolus vulgaris*) leaves, which showed that  $NH_4^+$  supply (2 mM) does not affect the operation of photosynthetic protein complexes [28] and therefore does not affect leaf  $CO_2$  assimilation capac-

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