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Physiological and molecular mechanism of nitrate uptake and assimilation in plants-a review

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Abstract
Nitrogen is one of the most essential elements because of its functioning in plant metabolic activities. Among different available forms of nitrogen, the nitrate form was widely available in aerobic soils. Besides, having a positive role of nitrate nitrogen on crop productivity its increased application is prone to heavy losses *viz.* leaching etc resulting in lower nitrogen use efficiency. Hence in this review different physiological and molecular mechanisms of nitrate uptake was discussed briefly under several sub mechanisms starting from response of root towards external nitrate concentration followed by signaling Mechanism involved in activation nitrate influx proteins. In addition, fate of absorbed nitrate in the plant body was also briefed to help in understanding the mechanism and different transports and genes involved. These insights primarily focus on advancement of biotechnology which would help in developing a fertilizer responsive transgenic plant. Further, when these plants are managed ideally with modern tailored approach of nutrient management might have a wider scope to unravel an ideal strategy to narrow the gap between actual and potential nitrogen use efficiency.

Keywords: nitrate sensors, nitrate signaling, nitrate assimilation, nitrogen use efficiency

Introduction

Nitrogen is one of the most essential macronutrients that plays a significant role on influencing the crop yield (Leghari, *et al.*, 2016) [30]. Although nitrogen is most abundant in the atmosphere but only nitrate and ammonium forms of nitrogen are available to plants. Unlike other nutrients mineralization of rocks shall not contribute to soil nitrogen status and usually applied externally either in the form of organic matter or chemical form (Grzyb, *et al.*, 2020) [17]. It is evident from green revolution that with the increase in rate of application of nitrogen the productivity of fertilizer responsive crop will substantially increase.

However, more than 60 to 70 per cent of nitrogen is lost through either leaching, denitrification and volatilization out of the total quantity of nitrogen fertilizer applied thereby leading towards serious environmental threats *viz.* eutrophication, GHG production, nitrate pollution etc (Mahmud, *et al.*, 2021) [33]. Beyond this over and indiscriminate use of nitrogen also raises the cost of production as this would attribute to serious pest and disease infestation (Carreras Navarro, *et al.*, 2020) [5]. Henceforth, understanding the mechanisms involved in nitrogen uptake shall be of prime importance in unravelling the ideal strategy for improving nitrogen use efficiency.

Among the available forms of nitrogen, nitrate form is most abundant in the agricultural systems (Vekaria, *et al.*, 2015) [47]. Besides, its essentiality in plant metabolism it is involved in signal transduction influencing the gene expression in root architecture. In this review, the different mechanisms involving sensing and transport of nitrate in plants, nitrate role in signaling transduction, nitrate assimilation, nitrate relocation and nitrogen storage and remobilization were briefly discussed.

Mechanism of Nitrate Sensing and Transport in Plants

Nitrogen is one of the most essential macro-nutrient which is available to plants as nitrate and ammonium form (Gojon, 2017) [16]. The nitrate form of nitrogen is the most dominant and abundantly available in well-aerated soils (Mukherjee and Sarkar, 2020) [36]. Therefore, understanding the nitrate uptake mechanism is key to improve nitrogen use efficiency (Chen, *et al.*, 2020) [6]. Nitrate sensing is a primary and fundamental step in the nitrate assimilation pathway initiating the uptake of nitrate ions into the plant from an external solution (Ali, 2007) [2]. According to a hypothesis in bacteria, nitrate reductase enzyme is evidenced to be nitrate sensor (Khodashenas, 2015) [24]. Further, the NR sensor senses the nitric oxide in the external medium when exposed to nitrate ions and upon exposure plasma membrane-based enzyme system gets activated and produces nitric oxide from nitrate which in turn elicits nitrate uptake system bound to the plasma membrane, However, unlike bacteria plant membranes are devoid of specific nitrate sensors on the membranes (Sun, *et al.*, 2015 and Siliakus, *et al.*, 2017) [44, 42]. In this context, certain integral proteins are widely recognized as they act as sensors and transporters simultaneously (Conde, *et al.*, 2010) [7]. Till date only four such nitrate transporter families *viz.* nitrate transporter 1 and 2 (NRT 1 and NRT 2), slowly activating anion channel (SLAC) and chloride channels were identified (Hsu and Tsay, 2013) [19]. Studies indicated the presence three systems depending on the concentration of external medium and nitrate inducibility (Liu, *et al.,* 2014) [31]. At low nitrate concentration transport is facilitated through high affinity transport system which are of two types constitutive and inducible, respectively while at high concentration of nitrate in external solution low affinity transport system (LATS) was reported to enhance the uptake of nitrate ions, However, the scope was further increased with the identification of molecular components associated with three transport systems (Krapp, *et al.* 2014 and Saber manesh, *et al.,* 2017) [25, 39]. The members of NRT 1 and peptide transporters are considered to function as low affinity transport systems and members of NRT 2/ nitrate nitrite transporters function as high affinity transport systems (HATS) (Okamoto, *et al.,* 2003) [37] NRT 1.1 and 2.1 were reported to involve ATP dependent root nitrate uptake by encoding proteins in low affinity and high affinity transport systems, respectively (Laugier, *et al.,* 2012) [27]. Among them, at low nitrate concentration in the external medium NRT 2.1 was evidenced to uptake nitrate through plant roots efficiently compared to NRT 1.1 (Glass, 2009) [14]. These proteins are symporters henceforth, an influx of nitrate was reported to be accompanied by a proton facilitated through H^+ ATPase enzyme (Yuan, *et al.,* 2017) [51].

Similarly, the latest pieces of evidence suggested that primary sensing and transport of nitrate might occur in plant leaves too. This is a mechanism through which fertilizers were up-taken through foliage when applied as a foliar spray (Abo-Sedera, 2016) [1]. The nitrate uptake into the foliage was reported to be reduced to ammonium without the involvement of long-distance transport through xylem hence helps in overcoming nitrate deficiency in leaves with less energy involvement, respectively (Zhang, *et al.,* 2018) [53].

Nitrate Signaling and Transduction

Nitrate signaling and transduction are one of the most complex processes (Zalutskaya, *et al.,* 2018) [52]. Nitrate responsive genes on the plasma membrane of the root cell initiate the process of nitrate signaling. Protein kinases and calcium play a key role in nitrate signaling. Calcineurin B like protein (CBL 1/9) and CBL interacting protein kinase 23 (CIPK 23) complex phosphorylate NRT 1.1 at low nitrate concentration in the external solution resulting in imparting NRT 1.1 as a high-affinity nitrate transport (Gao, *et al.,* 2018 and Wang, *et al.,* 2018) [13, 49]. Furthermore, phosphorylation of NRT 1.1 activates phospholipidase C which in turn activates several transcriptional factors present in both cytoplasm and nucleus primarily responsible for initiation and growth of the lateral root (Singh *et al.,* 2009) [43]. Similarly, another pathway of nitrate signaling under high concentration of nitrate in the surrounding and deficient in the cytosol is non-phosphorylated NRT 1.1 signal gets activated in the presence of non-threonine 101 phosphorylation resulting in induction of secondary messenger calcium which plays an important role in activation of CPK10 and NLP 7 complex in the cell nucleus, thus responsible for the production of assimilatory nitrate reductase (ANR) attributing towards lateral root initiation and growth (Wan, *et al.,* 2019 and Curran, *et al.,* 2011) [48, 8]. Conversely, AFB 3 an auxin response pathway is more consistent due to the non-involvement of PLC and Ca as a secondary messenger (Scherer, 2011) [41]. Studies indicated that the response of AFB 3 and NAC 4 transcription factor depends mainly on the functioning of NRT 1.1 in nitrate transport. This activation of auxin is responsible for primary root growth and lateral root growth which thereby facilitates enhancement in the uptake of nitrate (Overvoorde, *et al.,* 2010) [38]. However, in the presence of a low concentration of nitrate NRT 1.1 downregulates the auxin response thus ultimately affects the production of lateral roots significantly influencing the nitrate uptake from the external medium (Tahir, *et al.,* 2021) [45].

Nitrate Assimilation

The amount of nitrate that managed to pass across the plasma membrane by different nitrate uptake mechanisms into the plant system was destined to get translocated to different plant parts facilitated by specific nitrate transporters (Fan, *et al.,* 2017) [10]. The nitrate soon after translocation assimilates into very useful biomolecules *viz.* amino acid, protein etc. In comparison, a very high proportion of nitrate assimilation occurs in the shoot over the root which might be attributed due to more availability of energy generated by photosynthesis, respectively (Khan, *et al.,* 2019) [23]. Nitrate assimilation was rapidly reported to occur in both cytosol and chloroplasts this might be due to the presence of nitrate reductase enzyme usually present on plasma membrane and to some extent in cytosol too (Ali, 2020) [2]. The nitrate when comes in contact with NR enzyme the nitrate will get reduced into nitrite. The nitrite form of nitrogen will get easily transported into the chloroplast to fulfill the enzyme requirement for further reduction into an amino acid. Further, the amino acid created in the previous step undergoes reduction in the presence of an enzyme glutamine synthase resulting in the formation of glutamic acid, respectively (Bowsher, *et al.,* 2007) [4].

There are two genes which are mainly responsible for nitrate assimilation in plants namely GS1 and GS2 (Masclaux-Daubresse *et al.,* 2010) [34]. Their role is mainly governed by the concentration of nitrogen. Under high nitrate concentration GS1 plays an important role in nitrate assimilation into amino acids and additionally contributes in loading the phloem at source with nitrogen assimilates facilitating efficient utilization of assimilates in plant metabolic activities (Foyer *et al.,* 2011) [12]. On the other hand, GS2 take part both in direct nitrate assimilation and in assimilation of nitrate during photorespiration. However, assimilation is directly related to the concentration of nitrate taken up in the medium (Jauregui, *et al.,* 2015) [22]. In case of high concentration of nitrate in the medium the nitrate gets translocated to shoot assimilation of nitrate occurs in shoot while if the concentration of nitrate is low then translocation of nitrate is restricted thereby resulting in assimilation in the root. Hence, understanding the insights of nitrate assimilation is important to devise an appropriate strategy for improving the crop nitrogen use efficiency (Hirel, *et al.,* 2011) [18].

Nitrate Relocation

The nitrate that is up-taken into the root cells depending on the nitrate concentration of the cell sap relocation of nitrate occurs through xylem (Liu, *et al.,* 2014) [32]. As this process of nitrate relocation to the shoot is evidenced to be mediated by low affinity transporters hence concentration of the cell sap with respect to nitrate determine this process significantly (Dodd, *et al*., 2003) [9]. In general, nitrate relocation is mainly mediated by NPF 7.3 under normal condition while during salt stress NPF 2.3 was found to mediate relocation, respectively. However, nitrate uptake although occurs mostly in root but it should not be ignored to consider the contribution of leaf. Nitrate up-taken through leaf initially stored in the vacuoles and later relocation occurs from order leaves to new young leaves depending on the leaf nitrate requirement (Le Deunff, *et al.,* 2019) [29]. Under normal condition the nitrate transporters responsible for phloem loading to facilitate relocation were NPF 1.1 and NPF 1.2. While under starvation high affinity transporters like NPF 2.4 and NPF 2.5 plays a key role in efficient relocation of adequate quantity of nitrate (Fan, *et al.,* 2009) [11].

Nitrate storage and remobilization

Nitrate is very essential for growth and development of a plant but very high concentration of nitrate in the cell sap might be detrimental (Yosoff, *et al.,* 2015) [50]. Although, assimilation of nitrate in the cytosol help in regulating the concentration of the nitrate in the cell but in case over expression of nitrate transporters assimilation of nitrate could not be able enough to keep up the pace resulting in imbalance and higher nitrate concentration (Glass, *et al*., 2002) [15]. This occurs every now and then in plants hence to counter nitrate toxicity, plants have an alternate mechanism *viz.* cell storage mechanism. Cell vacuole is the major cell organelle facilitating the nitrate storage (Isayenkov, *et al*., 2014) [21].

As soon as with fall in nitrogen concentration in the cell sap the stored nitrate will be remobilized and subjected to assimilation (Inkham, *et al*., 2011) [20]. However, nitrate transporters involved in storage were not yet identified. However, it is clear that concentration of nitrate in cytosol is many times higher than the cell nitrate concentration and thereby significantly contributes in cell osmotic adjustment which is key mechanism in tolerating drought (Meloni, *et al.*, 2004) [35].

Under severe nitrogen deficiency where nitrate release from storage is insufficient to cater the crop needs then nitrogen based assimilates present in the form of biomolecules *viz.* proteins, amino acids etc. will undergo degradation and nitrogen remobilization begin to occur (Zhao, *et al.,* 2005) [54].

Future Perspective

Nitrogen is the most essential macronutrient for plant growth and metabolism. Increase in response of hybrids motivating farmers to apply more to gain more. However, heavy application of nitrogen is detrimental both economically and environmentally. Nitrogen use efficiency is the amount of nitrogen uptake by the plant per unit nitrogen applied. Nitrogen use efficiency is influenced by multiple factors *viz.* both genetic and managerial. Devising a strategy solely based on crop management aiming to limit losses of nitrogen is not ideal as in this case only external factors affecting the plant growth were considered but the plant internal factors were neglected which are having a true potential to influence utilization of nitrogen rather than minimization of losses. Thus clear understanding of mechanisms involved in nitrate assimilation pathway and the role of different genes involves in each and every step of assimilation is a key that helps in introduction of new transgenic genotypes using advanced molecular techniques which when accompanied with an ideal management strategies might enhance the nitrogen use efficiency of the crop**.**

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