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An update status on efficiency of nitrogen use in plant and factors affecting it

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Abstract
Over the past few years, research on plant nitrogen nutrition has had an immense impact. This review highlights research topics relevant to the functioning of nitrogen transporters beyond nitrate and nitrogen transporter signalling and sensing during plant development especially root development. It also illustrates different variables in order to increase the performance of nitrogen use, along with plant adaptation mechanisms.

Introduction

Plants cannot grow or develop without nitrogen. Global agricultural productivity has increased as a result of the continuous industrial production of synthetic ammonia.(Cui et al., 2018). Production of nitrogen fertilizer in industry involves huge energy cost and more than half of the applied nitrogen fertilizer goes waste in agriculture (Zhu et al., 2016) and cause negative effects on the health of human and environment. Thus it essential, to develop crop plants which use nitrogen efficient i.e. produce great yield with reduced N input (Garnett et al., 2015).“Several approaches are utilized for sustainable agriculture, including the use of slow-release fertilizers, biofertilizers, and legume-based rotation. (Cui et al., 2018) or select varieties with lower nitrogen requirements (Swarbreck et al., 2019) are used.Plant nitrogen efficiency is defined by the amount of nitrogen added to the plant seed production and often includes both nitrogen uptake efficiency and nitrogen physiological (assimilation) efficiency..(Moll et al., 1982). The uptake efficiency of nitrogen is the nitrogen acquiring capacity of nitrogen by root from the soil, which is determined by the availability of nitrogen in soil and use of nitrogen fertilizer as well as availability of water in rhizosphere, nitrogen assimilation processes and metabolite levels in plant and adaptive plasticity of root morphology and architecture towards nitrogen.”Nitrogen efficiency indicates the fraction of acquired nitrogen converted to total plant biomass and/or grain yield by plant (Stahl et al., 2016).Because the primary goal of increasing nitrogen utilization efficiency is to maximize crop yield potential with little nitrogen input, the molecular mechanisms involved in nitrogen metabolism and transport networks for its distribution must be studied. Understanding the mechanics of plant adaptation to fluctuating nitrogen sources has aided research into the molecular mechanisms of nitrogen utilization by plants and crop performance..(“Xu et al., 2012; Li et al., 2018”).

Nitrogen transporters: beyond transporters function

The external soluble nitrogen is taken up by root mainly in the forms of ammonium ($NH4^+$) and nitrate ($NO3^-$) in the rhizosphere and then redistribution and allocation of internal nitrogen on plants relay on the coordination of nitrogen transporters belonging to multiple families. Over past thirty year numerous research has been conducted which focus on understanding molecular mechanisms regarding acquisition of nitrate from soil, its transport and signalling to different tissues in plants (“Wang et al., 2018; Vidal et al., 2020”) help in understanding nitrogen use efficiency in plants (“Fan et al., 2016; Wang et al., 2018”). Wang et al. (2018; 2020) suggested that nitrate transporters are versatile in their function as they only help in nitrate transport but also in it internal distribution, nitrogen signalling , modulate root biome and maintain pH homeostasis of cells. Some nitrate transporters facilitates the transport of other substance such as Arabidopsis NPF6.3 or CHLORATE RESISTANT 1 (CHL1) or NRT1.1 which facilitates auxin and also regulate development of lateral roots (“Tsay et al., 1993; Lay-Pruitt and Takahashi, 2020; Maghiaoui et al., 2020”). Some nitrate transporters have dual function such as NPF6.3/ NRT1.1 which play significant role in transport and signalling of nitrate in Arabidopsis (Ho et al., 2009). OsNRT1.1B/OsNPF6.5 nitrate transporter modulates root microbiome and integrating nitrate and phosphate signalling via SPX4 protein (“Zhang et al., 2019 and Hu et al., 2019”). Except this, OsNRT2.3b transporter regulate nitrate uptake, cytosolic pH balance and increase yield in rice (Xu et al. 2012; Fan et al., 2016).

Another NRT2.1 transporter suppresses lateral root activation in response to nutritional signals (Little et al., 2005). OsNRT2.4 gene encodes a dual-affinity nitrate transporter and functions in root growth and nitrate distribution (Wei et al., 2018). Other NRT1/PTR “FAMILY (NPF) proteins recognise Arabidopsis thaliana that are capable of transporting both nitrate and organic molecules such as amino acids, gibberellic acid, ABA or secondary metabolites” (glucosinolates) (reviewed in Chiba et al., 2015). Amino acid transporters have been proposed to function as amino acid sensors (Dinkeloo et al., 2018). Above studied help in understand nitrogen

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signalling and uptake mechanism especially in vegetative phase and related to nitrogen acquisition by root from soil in form of nitrate or ammonium.(Hao et al., 2020). However overall mechanism of nitrogen utilization by plant, throughout life cycle is more complex because for temporary acquired nitrogen, root act a storage organ and from where organic nitrogen reallocated to sink organ during development of seeds, bud or shoot (Tegeder and Masclaux-Daubresse 2018).During vegetative to regenerative stage, expression profile of various NPF genes changes (Wang et al. 2020) and nitrogen signalling and sensing pathways involving in regulation of organic nitrogen transport mechanisms need further investigations.

Nitrogen signalling and sensing during development of plant

In response to external nitrogen supply fluctuations, plants may trigger complex regulatory networks to maximise nitrogen uptake and use (Xuan et al., 2017). Nitrogen signalling affect plant development by controlling seed germination, flowering time, stomatal movement as well as root and shoot architecture ("Osuna et al., 2015; Lin and Tsay, 2017; Araus et al., 2020; Jia and von Wirén, 2020; Luo et al., 2020"). Recently Liu et al. (2017, 2020) provide evidence about nitrogen signalling and sensing and suggested that nitrate activate "Ca2+ sensor protein kinases, calcineurin B-like protein-interacting protein kinases, and other protein kinases to triggers, intracellular calcium (Ca2+) signalling which in turn control primary root growth, early local responses of nitrogen and reflect nitrogen nutrient status of shoot" ("Liu et al. 2017, 2020; Jia and von Wirén, 2020").

Signalling from the root to the shoot which involves a small mobile peptide CEP derived from root and its receptor CEPR which express in shoot, helps the plant to adapt fluctuations in local nitrogen availability by regulate the expression of nitrate transporter NRT 2.1 in root (Tabata et al., 2014). Ohkubo et al., (2017) suggested that downstream component of CEP–CEPR pathway, CEPD move from shoots to roots, in response to nitrogen demand signal and activate NRT2.1 expression.("Chen et al., 2016"). Thus nitrogen induce mechanisms which regulate root development and growth are both diverse and complex and during it multiple pathways interact with each other based on the level of nitrogen supply and its form i.e. nitrate or ammonium ("Jia and von Wirén, 2020; Liu-B et al., 2020"). Nitrate also act as a signal to regulate the development of lateral root. In low concentration, nitrate has dual effects i.e. both stimulatory as well as inhibitory on the development of lateral root while high nitrate and nitrate heterogeneity supply has inhibitory and stimulatory effect respectively on lateral roots development (Sun et al., 2017). "For this development response, a MADS-box transcription factor ANR1 is essential which is present at the downstream of NPF6.3/NRT1.1 (Remans et al., 2006)." Recently, Liu Y et al. (2020), identified truncated MIKC-type MADS-box transcription factor called ZmTMM1 in maize which lacking C- and K-domains and reported that the localized supply of nitrate induced its expression preferentially in lateral root branching zone. Nitrate also regulates auxin biosynthesis as well as its downstream transport through nitrate transporter NPF6.3/NRT1.1 to regulate development of lateral root (Maghiaoui et al., 2020; Lay-Pruitt and Takahashi 2020). Aside from this, local ammonium ion supply causes higher order branching in lateral roots, implying an additional mechanism that aids in nitrogen uptake from soil, although excess ammonium ion supply inhibits root elongation and is hazardous to plants.(Jia and von Wirén, 2020). Genes which activated in response to ammonium ion are mostly AMOS1/EGY1-dependent and contain an ACGTG motif, a responsive element of abscisic acid (Li et al., 2012). Abscisic acid reducing reactive oxygen species and free ammonium ion through regulation of SAPK9–bZIP20 pathway in rice thus increase tolerance to high ammonium ion stress (Sun et al., 2020). In rice, Yang et al. (2019) identified that calcium sensor OsCBL1 regulate nitrate signalling and nitrate-mediated seedling growth and also modulates elongation of lateral root by affecting biosynthesis of auxin. Hu et al. (2020) also suggest association between nitrate signalling and auxin accumulation and biosynthesis for lateral root development in tea plant via transcription factors such as MYB genes. There are also various others transcription factors associated with nitrogen signalling and plant development as shown in table 1.

Table 1: Transcription factors associated with nitrogen signalling and plant development

Transcription factors associated with nitrate signalling	Family	Tissue Expression	Effect on Root	References
AtGRXS3/4/5/8/ROXY11	CC-type glutaredoxin (ROXY) family	Root and other tissue	Increased primary root length	Patterson et al., 2016
RAV2	Ethylene-responsive element-binding protein family	Root and other tissue	Genotype based Shorter lateral root length to both high and low NO_3^-	Gaudinier et al., 2018

CEPD2	“CC-type glutaredoxin (ROXY) family”	“Root, root endodermis, root vascular system”	Regulate the efficiency of root N acquisition	Ota et al., 2020
HMGB15	“AT-rich interaction domain-containing transcription factor family”	“Root and other tissue”	Larger lateral roots response to nitrate deprivation	Gaudinier et al., 2018.”
PAP2/MYB90	“MYB domain transcription factor family”	unknown	Trichome and root hair organogenesis	Rubin et al., 2009; Bielecka et al., 2015
BBX16	Constans-like zinc finger family	unknown	Total LRs length	Gaudinier et al., 2018

Factors affecting plant nitrogen status:

Abiotic stresses and limits on soil nutrients are significant environmental factors that reduce plant growth, production, and quality. Mechanisms have developed to interpret these environmental threats.(Gong et al., 2020). Nitrogen nutrients affect the growth and development of plasticity of both vegetative and reproductive organs (Luo et al., 2020). In general, the amount of water available in the soil has a substantial impact on nitrogen availability.(“Araus et al., 2020; Plett et al., 2020”). “Nitrate acquisition efficiency of root is affected by both water availability and rhizosphere pH” (Xuan et al., 2017). Thus these studies recognise the interactions between water availability in soil and nitrogen response in plants. Araus et al. (2020) provide evidence about the molecular signalling pathways which respond to both nitrogen and water. “Ishikawa-Sakurai et al. (2014) proposed that the expression of root-specific rice aquaporin genes OsPIP1.1, OsPIP2.3-2.5, OsTIP1.1-1.2, and OsTIP2.2 are positively correlated with the availability of nitrogen and nitrogen starvation contributes to reduced levels of aquaporin gene expression, weakening root hydraulic conductivity”. Similarly, disturbance of NRT2.1 nitrate transporters has negative effects on the transcript abundance of “PIP1.1, PIP1.2, PIP2.1, PIP2.3 and PIP2.7” aquaporins resulting in decreased root hydraulic conductivity (“Li et al., 2016”). Arai-Sanoh et al. (2014) stated that DEEPER ROOTING 1 (DRO1) locus, regulates root tip cell elongation and DRO1 lines improved water uptake and higher nitrogen uptake in some cases, resulting in higher grain yield.(Sun et al., 2017). Besides water availability, nitrogen-dependent signals also affected by other nutrients like potassium and phosphate (“Jia and von Wirén, 2020”).Several recent investigations have discovered connections between nitrate and phosphate signaling pathways, both of which are critical in plant growth and physiology.(“Maeda et al., 2018; Medici et al., 2019; Hu et al., 2019”).

Photorespiration also affects nitrate assimilation in shoot of both monocotyledonous and dicotyledonous species. (Rachmilevitch et al., 2004). Similarly,extreme climates like heat, dark-induced senescence, low nitrogen content in soil, drought and pathogen infection may disturb nitrogen use efficiency, seed composition and nitrogen remobilization efficiency in Arabidopsis (Marmagne et al., 2020). Except this root microbes also affect plant growth and increase nutrient availability.Bloch et al. (2020) and Dellagi et al. (2020) suggested that free-living diazotrophic bacteria and arbuscular mycorrhiza fungi are major soil microbes which improve nutrient uptake by plants and their growth. Recently Wang SS et al. (2020) reported that mycorrhizal colonization induce the expression of nitrate transporter gene OsNPF4.5, ZmNPF4.5 and SbNPF4.5 in roots of rice, Zea mays and Sorghum bicolor respectively.As a result, it is asserted that the NPF4.5 nitrate transporter is required for mycorrhizal nitrate uptake. Dellagi et al. (2020) hypothesized that interaction with beneficial bacteria such as Azospirillum, Azotobacter, and Bacillus, as well as fungi such as arbuscular mycorrhizal fungi, increases the nitrogen content of plants.

Conclusion

To maintain sustainable food production that meets the demands of the world's growing population, it is critical to develop crop kinds that are tolerant of harsh environmental circumstances and capable of making good use of

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the ecosystem's nutrients and water resources.The genetically inherited characteristics associated with nitrogen consumption performance are critical for a number of solutions for nitrogen fertilizer reduction in sustainable agriculture.

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