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Reviews and Progress Open Access

Research Progress of Urea Transporter DUR3 in Plants and Fungi

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Abstract Nitrogen is the largest mineral nutrient required by plants, and it is the main factor restricting plant growth and development. At present, plants have evolved different strategies to response changes of nitrogen in the soil, in order to ensure adequate nutrition and nitrogen supply. DUR3 family urea molecules are important intermediate products in the process of nitrogen metabolism in organisms. In plants, DUR3 family proteins co-transport urea and protons with high affinity. It plays a vital role in the nitrogen metabolism of plants. In addition, DUR3 family proteins can not only transport urea but also participate in the transport of polyamines in fungi. This review introduces the current research progress of DUR3 family genes. focusing on the *Arabidopsis* urea transporter *AtDUR3* and yeast urea transporter *ScDUR3.* It is hope to provide a theoretical basis for studying the role of the urea transporter DUR3 family in the process of nitrogen metabolism, and provide a reference direction for the next research of the urea transporter DUR3 family.

Keywords DUR3; Urea Transporter; Urea; Polyamine

Introduction

Plants are fixed organisms that cannot escape adverse environmental conditions. To conform to dynamic environmental challenges, plants must adjust their physiology, growth, and development. Maintain adequate nutrient supply under fluctuate environmental conditions is one of the most important challenges faced by plants (Kraiser et al., 2011). Nitrogen (N) is the most needed mineral nutrient, and its effectiveness is the main factor that restricting the growth of plants in natural and agricultural environments Nitrogen exists in the biosphere in various chemical forms. Molecular nitrogen accounts for 80% of the atmospheric composition. However, plants cannot directly utilize this form of nitrogen. Nitrogen enters the biological nitrogen cycle mainly in three ways: biological fixation, atmospheric fixation, and Haber Bosch industrial fixation to produce ammonia. Once nitrogen is fixed to nitrate or ammonia, it may have two main fates: Nitrate and ammonia can undergo a biochemical process and be converted back to N_2 (Sanhueza, 1982); Alternatively, they can be reduced or absorbed for the biosynthesis of nitrogen-containing metabolites. Amino acids, urea, small peptides, and other nitrogen-containing biomolecules can be released back to the environment through secretion, excretion, or decay of organic matter. These organic forms of nitrogen can also be used as nitrogen sources by plants and other organisms (Jones et al., 2005).

Urea is excreted into the environment by various organisms and is an easily available nitrogen source in soil. In addition, urea is one of the main forms of nitrogen fertilizer in agriculture, and it is also an important nitrogen metabolite in plants. Physiological experiments show that plant roots can directly absorb urea from soil (Gerendas et al., 1998). In the soil, urea is rapidly degraded into ammonium and carbon dioxide by urease (A nickel-dependent enzyme synthesized and released by microorganisms) (Watson et al., 1994). Urea is highly sensitive to the enzymatic degradation of urease. Urease is one of the most persistent enzymes in nature and can be widely expressed by most organisms (Polacco and Holland, 1993).

In the fungi *Saccharomyces cerevisiae* (*ScDUR3*), *paxilus involutus* (*PiDUR3*), *Aspergillus nidulans,* and *Candida albicans* (*CaDUR3*), *Arabidopsis thaliana* (*AtDUR3*) and *oryzam* (*OsDUR3*) ,Members of the urea / H^+symporter

group have been functionally characterized. They share 35-74% pairwise sequence identity, most of which include 14-15 predicted a-helix transmembrane fragments (TMS) (Sanguinetti et al., 2014). According to EST collection and database searches in genomic DNA, only one DUR3 homologue can be identified among all plant species investigated so far (Kraiser et al., 2011). The study of DUR3 homologs in plants shows that DUR3 homologs have a high affinity for urea transport (Kojima et al., 2007), and DUR3 family proteins as the main transporters related to urea absorption, have an important impact on plant nitrogen absorption and growth. In addition, in fungi, DUR3 homologues are also associating with polyamine uptake (Uemura et al., 2007). This review summarized the research progress of DUR3 family proteins in plants and fungi.

1 Research Progress of Plant Urea Transporter DUR3

The *Arabidopsis* urea transporter *AtDUR3* belongs to the family of sodium solute transporters. *AtDUR3* is predicted to encode a complete membrane protein with 14 transmembrane domains, and its N-terminal and C-terminal extend into the extraplasmic space (Schwacke et al., 2003). Phylogenetic analysis of *AtDUR3* and the 22 most homologous and characteristic amino acid sequences from BLAST searches showed that DUR3 proteins from plants and yeast have relatively high similarities, and all these sequences belong to sodium solutes The superfamily of symporters (SSS) (Sanguinetti et al., 2014). The SSS family currently including more than 100 members of prokaryotes and eukaryotes (Jung, 2002). Some of which are described as transporting sugars, amino acids, nucleotides, inositol, vitamins, ions, phenyl acetate, water, and urea (Saier, 2000). The membrane protein fraction of *Arabidopsis* root was analyzed by western gel blot to study the intracellular localization of *AtDUR3*. In the microsomal membrane fraction of *Arabidopsis* Columbia wild-type roots, antibodies against 14 amino acids at the C-terminal of *AtDUR3* were detected at approximately 55 kDa. It Corresponds to the expected size of protein hydrophobicity, which indicates the plasma membrane localization of *AtDUR3* (Kojima et al., 2007).

Under low nitrogen conditions, plants regulate root structure and absorption activity to improve the absorption of local and systemic nitrogen signals (Kiba et al., 2018). Studies have found that *AtDUR3* gene expression is up-regulated in the absence of nitrogen (Kojima et al., 2007). When adding urea to nitrogen-deficient plants, it was found that the level of *AtDUR3* mRNA in roots was significantly up-regulated. It even exceeds the level of transcripts in nitrogen-deficient plants. (Lejay et al., 1999). Through the phenotype analysis of the two T-DNA insertion lines, it is found that *AtDUR3* plays a role in the uptake of urea from the external medium. When ammonium nitrate is used as the only nitrogen source, there is no obvious manifestation of growth defects, which indicates that the genetic mutation in *AtDUR3* generally does not affect the acquisition of ammonium or nitrate. The functional expression of *AtDUR3* enhances the accumulation of intact urea molecules, indicating that *AtDUR3* can obtain externally supported urea in plants. (Kojima et al., 2007).

Increased protein degradation is a characteristic of leaf senescence. This results in the conversion of arginine into ornithine and urea in the mitochondria, thereby enhancing the production of urea (Witte, 2011). The plant entered the growth stage, the concentration of urea in *Arabidopsis thaliana* leaves increased with the increase of plant age and leaf age. This increase parallels the increase in the transcription level of the progeria marker gene ORE1. Similarly, a higher urea concentration was also measured in the old leaves under the rice leaves. These observations indicate that as long as the leaf nitrogen metabolism changes, the urea concentration will rise, and protein degradation and urea release have begun (Wang et al., 2012). In *Arabidopsis* native plants, it was observed that the levels of Asp and Glu were relatively reduced in senescent leaves, while the proportions of GABA, Leu and Ile increased especially with the increase of plant age (Diaz et al., 2005). Through studying the role of DUR3 and urea in nitrogen reactivation. It was found that during natural leaf senescence, the urea concentration and DUR3 transcription level increased in parallel with the senescence marker ORE1 in a plant age and leaf age-dependent manner. The lack of DUR3 reduced the accumulation of urea in the leaves, while the loss of urea in the apoplasts of the leaves increased. It is concluded that urea can be used as an early metabolic marker of leaf senescence, and DUR3-mediated urea recovery is helpful to the re-transfer of urea nitrogen during leaf senescence (Bohner et al., 2015).

Phylogenetic analysis shows that the putative DUR3 protein is closely related in monocotyledonous plants, such as corn, rice, wheat, barley, and millet, and has more than 80% homology at the amino acid level (Zanin et al., 2014). Studies have found that in maize, the urea transport of *ZmDUR3* in yeast and *Arabidopsis* plants, the regulation of its transcription by nitrogen, its target of PM, and the appearance of *ZmDUR3* mRNA associated with phloem tissue, strongly suggest that *ZmDUR*3 is an active urea transporter protein. *ZmDUR3* plays a role in capturing urea as a nitrogen source, especially under nitrogen deficiency conditions. And in the senescent organs of plants, nitrogen is reused in the form of urea. *ZmDUR3* improves plant growth under low-urea conditions by increasing the net urea absorption expressed in *Arabidopsis* (Liu et al., 2015). Through the functional characterization of *OsDUR3*, a high-affinity urea transporter in the transport system rice, in crops. It was found that *OsDUR3* encodes a complete membrane protein, containing 721 amino acid residues and 15 predicted transmembrane domains. Heterologous expression showed that *OsDUR3* restored the growth of yeast DUR3 mutants on urea, and 10μM quantitative reverse transcription-polymerase chain reaction (qPCR) analysis in Xenopus oocytes showed that urea supplemented conditions after and after nitrogen deficiency The expression of *OsDUR3* in rice roots was up-regulated. Moreover, the overexpression of *OsDUR3* supplemented the *Arabidopsis* atdur3-1 mutant, improved the growth under low urea conditions, and significantly increased the absorption of urea by roots system. Combined with its plasma membrane location detected by the green fluorescent protein (GFP) label, and the result of T-DNA destruction of *OsDUR3*, which reduces rice urea growth and urea absorption, a series of studies have proved that *OsDUR3* is an active urea transporter and plays an important role in the effective acquisition and utilization of urea in rice (Wang et al., 2012). Under nitrogen deficiency and field conditions, DUR3 contributes to nitrogen transport and rice yield (Beier et al., 2019). By analyzing the differential expression of the *CaDUR3* gene of coffee plants under different abiotic and biotic stresses, it was found that the expression of *CaDUR3* increased in leaves under water deficit and heat stress, but decreased in plants under salt stress. When infected (Coffee rust), *CaDUR3* is significantly up-regulated at the beginning of the infection process of disease-sensitive and disease-resistant varieties. These results indicate that in addition to urea acquisition and N-reactivation, the *CaDUR3* gene may be closely related to response various stress (Dos et al., 2021).

In algae, the maximum likelihood tree was constructed using *dinoflagellates* DUR3 and other eukaryotic DUR3 protein sequences. In the MMETSP database, DUR3 protein sequences have been found in almost all the transcriptome of *dinoflagellates,* which are in the form of a large number of part homologous sequences. Many studies have identified as many as three DUR3 parahomologues in certain types of red algae and green algae (Kakinuma et al., 2016). These genes of *dinoflagellates* are cluster into different branches and have an evolutionary relationship with other known DUR3 genes of microalgae. Evaluation of the expression level of DUR3 gene by RT-qPCR revealed their sensitivity to the nitrogen input under study. After supplementing with additional nitrogen source, the expression level of DUR3 was down-regulated. (Pechkovskaya et al., 2020). Reverse transcription-quantitative PCR analysis showed that the expressions of high-affinity NO_3 transporter (NIT), NH_4^+ transporter (AMT), and high-affinity urea active transporter (DUR3) were significantly up-regulated under N-restriction compared with N-rich control. The mRNA levels of AMT and DUR3 also showed a significant circadian rhythm, with higher levels at midnight (Ji et al., 2020).

2 Research Progress of Fungal Urea Transporter DUR3

At low concentrations, urea is imported into yeast through an ATP-dependent sodium urea transporter encoded by the NCR sensitive DUR3 gene, (Sumrada et al., 1976). In addition to its role as a urea intake, *Saccharomyces cerevisiae* DUR3 with 16 or 12 transmembrane fragments (Kashiwagi and Igarashi, 2011) has been proven to promote the uptake of polyamines, which are very important for cell growth. In fact, excessive polyamines lead to the inhibition of DUR3 mRNA (Uemura et al., 2007), which indicates that cells regulate the expression of DUR3 in response to urea and polyamines. Cellular urea can be further degraded to carbon dioxide (CO_2) and ammonia (NH_3) by the urea amylolytic enzyme (Dur1, 2p), or secreted by the urea membrane transporter Dur4p. Another important urea transporter Dur3p is also involved in urea uptake (Zhang et al., 2017). By monitoring the uptake of the Anthracycline adriamycin into yeast cells, it was demonstrated for the first time that the yeast plasma

membrane protein Agp2, which controls the expression of DUR3 and SAM3, is necessary for drug uptake. The deletion of DUR3 and SAM3 genes reduced the uptake of adriamycin, but the deletion of both genes did not reduce, while Δ Agp2 mutant was severely damaged, indicated that Δ Agp2 controls drug uptake through DUR3 and SAM3 and at least one additional transporter (Brosseau et al., 2015). In the brewing industry, ethyl carbamate (EC) is a potential human carcinogen, which is mainly produced by the spontaneous reaction between urea and ethanol during the brewing of yellow rice wine (Wu et al., 2014). Urea concentration directly affects EC content. Therefore, reducing the content of urea in yellow rice wine is the main way to reduce EC accumulation. Constructed an efficient CRISPR vector and applied it to the overexpression of DUR3. Overexpression of DUR3 reduced the contents of urea and EC in yellow rice wine, and the effect of overexpression of DUR3 on fermentation characteristics was negligible (Wu et al., 2020). However, somebody believe that overexpression of Dur1, 2, and DUR3 will produce excessive ammonium, which may affect the taste of wine (Zhao et al., 2014). In addition, DUR3 has been shown to regulate intracellular boron concentration, but the physiological significance of transport activity is unclear (Nozawa et al., 2006). DUR3 also seems to play a role in the transport of uracil and uridine, because several double gene knockout combinations show some phenotypic deviation on these media, although there is no change in a single gene knockout strain (Zhang et al., 2017).

DUR3 is the main urea transporter in *Candida albicans*. The direct induction of DUR3 by urea does not depend on its metabolism through the urea amylolytic enzyme Dur1,2, but the further slow induction of DUR3 requires the Dur1,2 pathway (Navarathna et al., 2011). *Candida albicans* contains six DUR transporter family members responsible for the uptake of polyamines (spermine and putrescine). DUR3 and DUR31 genes encode polyamine transporters and promote the uptake of histidine protease inhibitor 5 (Hst 5) (Tati et al., 2013). Though constructed gene deletion mutants for Candida albicans polyamine transporters Dur3、Dur31、Dur33、Dur34 and tested Hst 5 sensitivity and spermine uptake. find Spermidine uptake and Hst 5 mediated killing ofΔdur3、Δdur31 and Δdur3/Δdur31 strain decreased significantly; DUR3 overexpression strains increased Hst 5 sensitivity and spermidine uptake (Kumar et al., 2011). *Paxillus involutus* is an ectomycorrhizal basidiomycete, which can use urea as the only nitrogen source. Morel et al. (2008) reported the molecular characteristics of an active urea transporter (*PiDur3*) isolated from this fungus and proved that urea input is a small event under ammonium conditions, which is supported by the inhibition of *PiDur3* expression when the intracellular glutamine content is high. In contrast, for urea treatment that is not a preferred nitrogen source, pidur3 is more regulated by intracellular urea than glutamine. Using cDNA array analysis, compared the fungal gene expression levels corresponding to about 1200 expression sequence tags in the ectomycorrhizal root tip (ECM) of *Selaginella birch ectomycorrhizal* combination growing on peat and the connected free radical ectomycelium (EM) in the microcosmic system. It was found that 65 unique genes were differentially expressed in the two fungal flora. In ECM, genes encoding urea (Dur3) and spermine (Tpo3) transporters were up-regulated 4.1-fold and 6.2-fold in EM. In addition, it was found that urea was the main nitrogen-containing compound found in EM by gas chromatography-mass spectrometry. It was observed that genes homologous to urea transporter (Dur3) and allantoic acid uridine succinate transporter (Dal5) genes were up-regulated in EM, which may ensure the transfer of these nitrogen sources between hyphae (Morel et al., 2005). It was found that the inhibition of polyamine biosynthesis would lead to the accumulation of reactive oxygen species and the enhancement of itraconazole (ITC) sensitivity; During ITC induced stress, a slight increase in cellular polyamines was helpful for *Aspergillus fumigatus* to adapt to this stress; Consumption of tpo3 and/or dur3 leads to moderate accumulation of polyamines, which endows ITC tolerance by scavenging reactive oxygen species. This study will improve a new understanding of polyamine function and enhance the ability to control fungal pathogen activity and drug resistance (Chen et al., 2020).

3 Prospect

The role of nitrogen in production, life and the ecological environment has always been the focus all over the world. In-depth exploration of the relationship between nitrogen metabolism and plant physiology has a profound impact on agriculture and the environment, The urea transporter DUR3 plays a vital role in the nitrogen metabolism of plants. In order to deepen our understanding of the role of urea transporter in the nitrogen

metabolism pathway, it is necessary to explore the way the urea transporter DUR3 operates at the molecular level in higher-level tissues, to have a deeper understanding and elucidation of its in-depth signal pathways and molecular mechanisms of transport. Promote plants to obtain nitrogen in the natural or agricultural environment, this can not only increase yields, but also reduce the use of nitrogen fertilizers, thereby reduce greenhouse gases, stratospheric ozone, acid rain, and surface water and groundwater nitrate pollution, hoping to further promote the harmonious development of agriculture and the environment. In addition, DUR3 homologues are also related to the uptake of polyamines, which play a vital role in reducing the content of urethane and enhancing the ability to control fungal pathogen activity and drug resistance in the wine industry.

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