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Research Article

Role of Ion Transporters in Plant Responses to Abiotic Stress

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Abstract: Plants will be influenced by adverse external factors of the natural environment in the process of growth and development, including biotic and abiotic stress. Abiotic stresses such as high salinity, drought and heavy metals can cause metabolic disturbance, interfere with the normal growth and development of plants, in turn, lead to a drop in the quality of crops. Ion transport through the membrane transport protein to maintain the stability of ion concentration, ion in the cytoplasm of the relative stability is essential for normal growth of plants. Therefore, study on the ion transport protein has important practical significance in abiotic stress responses in plants. This study mainly introduces the recent research progress on the ion transporters involved in high salt, drought and heavy metal stress response, which will help to reveal the regulatory mechanisms under abiotic stress of ion transporters as well as provide evidence for the abiotic stress tolerance in plants.

Keywords: Abiotic stress, ion transporter, plant, stress response, transmembrane transport

INTRODUCTION

Abiotic stress such as drought, salinity, heavy metal pollution and mineral deficiencies, these will lead to the rapid increase of active oxygen substances in cells, proteins, lipids and the damage to DNA and the intracellular membrane structures, which affects plant normal growth, eventually leading to the reduction of crop quality. In abiotic stress, the three main factors that restrict the normal growth and development of plants are the major factors of salt, drought and heavy metal pollution (Wang *et al*., 2014). According to the statistics of relevant data, the world is currently concerned, nearly 22% of the arable land is over salt, salt stress damage to the irrigation of farmland is about 50%, in 2050, will have more than half of arable land salinization. Under adversity stress, the plant itself mainly through transfer abiotic stress signal, adjust the body's metabolic process to increase the degree of plants to withstand adverse external environment, thus contributing to the continuation of their own species.

In the process of adversity stress, plants for normal growth and development, its body gradually formed a certain adaptation mechanism, the plant drought resistance, resistance to salt and heavy metal research in recent years have gradually become a hot research in the field of Botany (Yuan and Yu, 2015). At the same time, because of the rapid development of molecular biology, people can have be able to analyze the resistance mechanism of plants to stress from the point of the view of the molecular and then to obtain the effective resistance genes and to cultivate a good variety of crops. This study mainly introduces the types and mechanisms of ion transporters in high salinity, drought, heavy metals, in order to provide clues and basis for further study of the regulation mechanism of ion transport proteins in plant response to stress.

PLANT ION TRANSPORT PROTEIN AND SALT STRESS RESPONSE

The soil salinity and salinity in China is increasingly serious and the soil salinity is the key factor to restrict the yield of crops. The main damage to the plant is the following two aspects: The first is that the excess salt makes the soil solute concentration is high and then leads to the loss of soil moisture and the survival rate of the plants and the normal metabolism (Ding *et al*., 2015). The second is the plant to absorb too much salt so that the proportion of K^+/Na^+ imbalance. According to the research, the plant's resistance to salt toxicity mainly includes the efflux of salt, reducing the absorption of salt in the outside world and the separation of salt and all of these have an inseparable relationship with the ion transport proteins in plants.

Plant transmembrane ion transport proteins involved in salt stress response: There are various membrane transporters in the cell membrane, which exist in different cell membranes in different forms, the following mainly describes the salt of the ion transport and associated membrane transport proteins.

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Table 1: The Na^+/H^+transporter proteins and their domains in plants

Plant	Gene symbol	The main existence part	Reference
Arabidopsis thaliana	*AtNHXl*	Vacuole membrane, Plasma membrane	Zhang *et al*. (2011)
Rice	*OsNHXl*	Vacuole membrane	Lin *et al*. (2012)
Wheat	*TaNHXl*	Vacuole membrane	Wang *et al*. (2013)
Citrus	*cN-HXl*	Vacuole membrane	Porat *et al*. (2002)
New Zealand	*TtNHXl*	Vacuole membrane	Zhou *et al*. (2009)
Corn	*ZmNHX*	Vacuole membrane	Mishra *et al*. (2015)
North Saltbush	*AgNHXl*	Vacuole membrane	Akira *et al*. (2001)

Plasma membrane Na^+/H^+ reverse transport protein: One direct pathway of plant resistance to salt toxicity is Na^+ in vitro. According to the study, the Na^+ in vitro was mainly related to the plasma membrane of Na^+/H^+ and this process is accomplished by the proton electrochemical gradient of ATPase H^+- produced by the plasma membrane (Golldack and Dietz, 2001). The Na binding region of the plasma membrane is a conserved Na^+/H^+ binding region and its amino acid sequence is not present in the Na pathway. The C-terminal is a long chain tail region. Transmembrane region and cytoplasmic tail region of Na^+/H^+ reverse transport proteins play a vital role in the function of the membrane.

In Arabidopsis thaliana, Jian-Kang *et al*. (2002) cloned *SOS1* gene, *SOS1* mainly located on the plasma membrane of leaves and roots, the gene is mainly used for encoding the Arabidopsis plasma membrane Na^+/H^+ antiporter and through a study found that the *SOS1* mutants of salt sensitive, thus indicating the *SOS1* plays a vital role in plants against salt stress forcing process (Ma *et al*., 2001). Further, it was found that *SOS1* gene sequence of the N terminus is highly hydrophobic and it contains 12 transmembrane regions and its C terminus contains about 700 amino acid residues and the hydrophilic, at the end of the tail it closes to the cytoplasm, through *SOS1* and regulation of reverse protein of many proteins interact to regulate Na^+/H^+ transport. In addition to the nhaA, the Na^+/H^+ of the plasma membrane of the plasma membrane was cloned from the Pseudomonas sp and the salt tolerance of soybean was greatly improved. The results show that the response of plants to the high salinity environment is the main Na^+ discharge cells, the process is mainly dependent on the plasma membrane of the Na^+/H^+ reverse transport proteins and ultimately enable the plant to adapt to high salt environment.

Plasma membrane Na^+ and K^+ ion transport proteins: Potassium is one of the elements which are necessary for the development of the normal growth of plants, it can promote the plant stems robust, improve fruit quality, greatly enhance the cold tolerance of the plants. The physiological and biochemical responses of potassium in plants have important effect on plant growth. Therefore, maintaining the high ratio of K^+/Na^+ can promote the growth of the plants. In the high salt environment, the K^+/Na^+ ratio decreased because of the increase of Na content, which was against the growth of plants. At present, it is believed that plants have two systems for the absorption of potassium: The first is the low affinity K uptake system, when higher concentrations of external potassium mediated potassium absorption, belongs to the passive absorption process needs to consume energy, whole process is mainly dependent on the K channel complete; the second is the high affinity potassium uptake systems, when the external potassium concentration is low mediated K absorption, rely mainly on the K vectors completed.

One of the main methods of plant resistance to salt stress is to maintain the high ratio of K^+/Na^+, the researchers began to try to obtain a certain K^+, Na^+ transporter protein, so that when plants under salt stress, they can be obtained by high affinity K^+ to maintain the relative balance of K^+/Na^+ ratio. The entry of Na^+ into plant cells is mainly based on the selective absorption of ions. Based on the cation transport system, plant cells show some selectivity to ion uptake and the system is composed of cell membrane and membrane transport proteins. In wild type Arabidopsis, through the study, Rus *et al*. (2001) found that the uptake of Na^+ in the roots of AtHKT1, from the above studies, we can infer that the *HKT1* transporter may have a critical application in plants under salt toxicity.

Vacuole membrane transport protein: There is a highly conserved binding site in the protein structure of the protein structure of the plant vacuole membrane and the induction effect of Na on the membrane transport protein gene is different from the site. The area of Na^+ is that the Na^+ is found in the vacuole. The accumulation of Na^+ by Na^+/H^+ in the vacuole is one of the important mechanisms of plant resistance to salt toxicity. At present, the research on Na^+/H^+ reverse transport proteins is relatively high (Table 1).

After cloning and transforming the Na^+/H^+ reverse transport protein gene of the plant, it was found that the single Na^+/H^+ reverse transport protein gene could significantly improve the plant resistance to salt stress. In addition, Zorb *et al*. (2005) found that the expression of *ZmNHX1* gene in Maize under salt stress was different.

Plant ion transport proteins involved in drought stress response: Throughout the ages, drought is a major disaster for human encounters, soil drought stress limits the output and quality of agricultural production, Zhang *et al*. (2015) through the peanut by drought stress experiment showed that peanut yield and quality were significantly decreased, the metabolic process also occurred disorder. Plants in the long-term evolution of the process, its body gradually formed resistance to drought stress control system (Saini *et al*., 2012). For example, in the process of drought stress, the plant itself induced the synthesis of a series of functional proteins to protect plant cells from damage (Shinozaki and Yamaguchi-Shinozaki, 2007; Wang *et al*., 2008). Ion transporters involved in plant response to drought stress in the main study, aquaporins.

Aquaporins: The structure features of plant aquaporin family is quite conservative, usually with four poly forms of existence, each monomer are able to form independent water channels. Aquaporin 6 transmembrane alpha connected by 5 short rings, a spiral into the cytoplasm of the N end and C end (Ruan *et al*., 2009). Currently known, people have learned aquaporin 18 structure characteristics, provide strong theoretical basis (Li *et al*., 2010) for aquaporins of water and solute permeability mechanism. And other need to consume a lot of energy compared to the active transport of ion channel, aquaporins is consume less energy, passive water transmembrane transport, with advantages of high efficiency, less energy consumption, therefore under drought stress, aquaporins can in a short period of time to transport water points make the plant body water balance and ultimately enable the plants to better adapt to the arid environment (Lei *et al*., 2005).

Aquaporins are usually located on the cell membrane, it is possible to high rate of selective transport of water molecules (Zhu and Zheng, 2005), will generally be divided to three categories: tip, MIP and NLM (Santoni *et al*., 2000). The Preston by using the Xenopus oocyte expression system in aquaporin function research, finally confirmed the transport of water channel protein on the cell membrane, is aquaporins. With the emergence of more and more homologues, aquaporin began to be named Aquaporin, referred to as AQP. General in the cell membrane, water channel protein mainly to four peptide dimer forms of existence, function monomer, both of them can be independent as a water channel protein, under normal circumstances, in plant water transport across the membrane is aquaporins.

Under water deficit bad conditions, plants can regulate intracellular solute concentration to maintain turgor (Villar *et al*., 2011) and through the active switch water transmembrane channels enable plants to the largest extent, reduce the loss of water and can absorb more moisture. In Arabidopsis, Maurel *et al*. (1993) and other researchers found the first aquaporin gamma γ-TIP in plants. The water channel protein is a encoding, 35, 33 and 36 genes in the genome of Arabidopsis, rice and maize, respectively. With the development of the experiment, the new aquaporins have been found to.

Plant ion transport proteins involved in heavy metal stress response: With the increase of the content of heavy metals in plants, the metabolism of plants in the plant is in disorder and the plant growth is inhibited. According to the relevant statistics in 2014, China's heavy metal cadmium pollution points exceeded the rate of up to 7% (The Environmental Protection Department, the Ministry of Land and Resources, 2014). In the long evolutionary process, the plant will form a protective mechanism to maintain its healthy growth. In Arabidopsis, *AtIREG2* may be involved in the transport of heavy metal Ni in cytoplasm and the overexpression of *AtIREG2* gene in transgenic plants was also improved by Ni tolerance (Schaaf *et al*., 2006). It was later found in the oat roots, Cd and the plant chelating agents to transport to the vacuole, thereby avoiding the heavy metal Cd on the oat injury (Zhan and Chen, 2011). Also found in Arabidopsis, the Zn^{2+}/H^+ transport protein MTP of the vacuole membrane was accumulated in the vacuole in excess of Zn^{2+}, to maintain the balance of intracellular Zn^{2+}. It was experimentally confirmed that the *AtMTP1* expression of Tanaka *et al*. (2013) was higher than that of wild type and the former could accumulate more Zn, so that the transgenic plants could grow better under high Zn environment. In addition, overexpression of PtdMTP1 in Arabidopsis could enhance the tolerance of Zn to Rajesh *et al*. (2012). Thus, the membrane transport proteins play a vital role in the detoxification of heavy metals in plants.

Metal element transport related proteins: When plants are subjected to metal stress, the plants in vivo binding proteins such as plant complexes, metal sulfur protein, can be combined with the metal, in the form of complex with proteins to be transported and through the organization of the trans membrane transport proteins in the body to accumulate (Table 2).

Natural resistance associated macrophage protein and cadmium stress response: Macrophages are immune cells. In recent years, experiments have demonstrated that the intracellular bacteria can survive in the macrophages not only depend on their own conditions and related genes, but also depend on the regulation of some genes of the host.

As a kind of family of membrane proteins, the natural resistance macrophage protein is a kind of protein which involved in the transport of two valence metal ions. It is found in animals and bacteria. According to the structure, function and distribution of two major categories: *NRAMP1*, *NRAMP2* (Forbes and Gros, 2003). The rice genome has 7 predicted *OsNRAMP* (Li-Juan and Long-Jun, 2011), which is shown in Table 3.

Table 2: Cellular localizations and function of the metal transporter proteins

Transporter protein	Metal	Cellular localization	Function	Reference
PCs	Cu Zn Cd	Cytoplasm	The formation of complexes in the vacuole.	Sobrino-Planta *et al.* (2014)
MTs	Zn Cd Cu	Cytoplasm	Formation complex	Kärenlampi *et al.* (2000)
Nramps	Mn Fe Cd	Vacuole	Absorption of heavy metals	Takahashi *et al.* (2011)
ZIP	Mn Zn Fe Cd	Plasma membrane	Transport inorganic cations to the root	Connolly *et al.* (2002)
ABC transporters	Fe Pc-Cd	Vacuole membrane	Adsorption of inorganic cations by chelating heavy metal	Rees *et al.* (2009)
Cation/H+antiporters	Mn Cd	Vacuole membrane	The concentration of metal ions in the cell fluid involved in the regulation	Hirschi *et al.* (2000)

Table 3: Domains and subcellular localizations of the natural resistance-associated macrophage protein

Geme name	Gene symbol	Function site	Subcellular localization	Reference
Natural resistance	*OsNRAMP1*	Root	Plasma membrane	Takahashi *et al.* (2011)
macrophage protein	*OsNRAMP3*	Root and leaves	Plasma membrane	Yang *et al.* (2013)
	OsNRAMP5	Root	Plasma membrane	Ishimaru *et al.* (2012)

According to the experimental results show that, rice *OsNRAMP1* in root mainly expression, the expression is closely related to cadmium exposure and accumulation ability and its overexpression can increase the accumulation of Cd in rice leaves. Experiments show that *OsNRAMP5* can help to absorb Mn^{2+}, Fe^{2+} and Cd^{2+}, which plays an important role in the growth and development of rice. After the *OsNRAMP5* gene was found, the rice yield was significantly decreased, especially in the low Mn2+ condition, but it was significantly higher than that in the Sasaki *et al*. (2012). In addition, Japanese researchers to obtain the gene mutants, by *OsNRAMP5* coding defects of transporter greatly reduced root Cd^{2+} uptake, thereby reducing stalk and grain Cd content (Ishikawa *et al*., 2012).

Low affinity cation transporter *OsLCT1* and cadmium stress response: Rice is the main food crops in China, so the accumulation of cadmium in rice grain is a threat to our health. The enrichment of cadmium in rice was accomplished by the transport of E *et al*. (2013) in the phloem, which was identified by the experimental results of a transport protein, called *OsLCT1*, which is located on the cytoplasmic membrane and is involved in the transport of Cd to rice grains.

In the yeast expression test showed that *OsLCT1* has the activity of extracellular transport. In rice plants, *OsLCT1* was expressed in stem and leaf of rice growing period and the expression of *OsLCT1* in vascular bundle cells and vascular bundle was also found. In the heterologous expression system, LCTl has some difference in the absorption of cations, which is low affinity for Na^{+} and Rb^{+} and Rb^{+} can prevent the uptake of Antosiewicz and Hennig (2004) from Ca^{2+}. The low affinity cation transport protein *OsLCT1* was localized on the plasma membrane and was in the upper part of the Cd^{2+} to carry (Uraguchi *et al*., 2011). In the control group, the content of Cd^{2+} in the control group was two times that of rice, but it had no effect on the contents of other metal elements and the growth of plants in the control group. The expression of *OsLCT1* gene in tobacco was found: In the condition of low Ca^{2+} concentration, the growth of transgenic tobacco was significantly better than that in control and the Ca^{2+} was accumulated in the stem and in the condition of higher Cd^{2+} concentration, the cadmium resistance of transgenic tobacco plants was significantly and the Cd^{2+} accumulation in root was lower than that in the control group (Martinka *et al*., 2014). The results indicated that Cd^{2+} was mainly in the phloem of the stem and the presence of *OsLCT1* could guarantee the accumulation of Cd and Cd in rice, which was beneficial to the selection of low cadmium species.

Membrane protein *IRTl* and heavy metal stress response: *IRTl* is an iron ion transport protein, which is located on the cytoplasmic membrane and has a high degree of similarity with *ZNTl*. It can be expressed in the root cortex, which can efficiently transport Fe, Zn, Mn and Cd, which is an important transporter protein and is regulated by ethylene signal transduction pathway.

So far, a new family ZIP gene family has been born since Eide *et al*. (1996). From Arabidopsis thaliana, a new family of *IRT1* gene family, which is a kind of two valence metal ion transporter gene family and the ZIP gene family has high homology. *IRTl* was isolated from Arabidopsis thaliana and then cloned into the ZIP family of two valence iron carrier genes, such as *IRT2* and other related experiments. It was found that the sensitivity of Cd^{2+} to *IRT1* was increased in yeast and this study showed that *IRT1* could absorb Cd and Cd stress decreased the damage of plants. The results show that *IRT1* can absorb Cd^{2+} and reduce the damage caused by Cd stress. With the cloning of *IRT1*, a number of genes associated with the encoding Zn^{2+} transporter associated proteins have been cloned. *ZIP2*, *ZIP3*, *ZIP4* and *ZIP1* were cloned in Arabidopsis. In Zn^{2+} deficient plants, the expression of *ZIP3* and *ZIP1* was promoted and their expression was inhibited by Vert *et al*. (2002) when Zn^{2+} was abundant. Thlaspi caerulescens also found a similar and *ZIP4* Zn translocator gene *ZNT1*, further prove that they might and Zn^{2+} absorption are closely linked.

CONCLUSION AND PROSPECT

In addition to salinity, drought, high and low temperature, heavy metals, there are many other non biotic stresses such as radiation, ozone and the response of plants to abiotic stresses. Stress factors cause the change of protein, which is involved in the response to stress by the way of participating in photosynthesis, energy metabolism, signal transduction, ion transport. Plant response to abiotic stresses is a mechanism for the adaptation of plants to adverse environmental conditions. Although the key role of plant ion transport proteins in non biological stress has been studied, there are still limitations: research materials are mainly model plants and the study on other important crops is less; control mechanisms have been further studied.

At present, the research on plant response to stress is mainly focused on the differences of the static index of stress and the research on the dynamic changes of plant in different stages of response to stress is not enough. With the development of molecular biology and the continuous development of plant salt tolerance, drought resistance and heavy metal mechanism, scientists can effectively merge advanced molecular biology and other aspects of molecular biology and traditional breeding and then set up the mechanism of stress induced expression in plants.

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