

The Classification, Isolation and Function of Amino Acid Transporters in Plants

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Abstract

Amino acid transporters (AATs) have essential roles in transport of a broad range of amino acids, which are indispensable in plant growth and development. While many putative AATs have been identified and the complete genomic sequences of the important plants have already been completed by splicing and assembling, there is still little known about the functions of different AATs and their effects on plants. Therefore, this study mainly reviewed the role of AATs in plants from three aspects: the classification, isolation and cloning of AATs and the functional research of AATs. This review would provide useful references for the utilization of AATs in staple food crops.

Keywords: amino acid transporter, classification, isolation, function

1. Introduction

Amino acids play an important role in the growth, development and metabolism of plants, which is because amino acids are the basic components of various enzymes and proteins in plants, and are precursors or nitrogen sources for nucleic acids, chloroplasts, hormones and secondary metabolites in plants, which are essential for the growth and development in plants. Amino acids can be synthesized by plastids, cytoplasm, mitochondria and peroxisomes in roots or leaf cells of plants, and plants can also absorb amino acids directly from the soil or ultimately convert inorganic nitrogen into amino acids. Nitrogen is one of the most important limiting elements factors for plant growth and development. In higher plants, the absorption and distribution of inorganic nitrogen are mainly in the form of NO_3^- and NH_4^+ . Inorganic nitrogen is directly transferred from roots or leaves to amino acids in the form of organic nitrogen transport. Amino acids are then transported to the plant's (roots, leaves, flowers, pollen and embryos). Ultimately, the number, size and quality of flowers and seeds depend on these amino acid transport processes (Lu et al., 2012). As the main form of long-distance transportation and distribution among tissues of nitrogen assimilation products in higher plants, amino acids are transported in plants through transmembrane transport to synthesize proteins and carried out corresponding material metabolism and signal transduction (Liu et al., 2018). AATs play an important role in amino acid transmembrane transport. Amino acids are directly or indirectly involved in plant nitrogen metabolism, which is very important for plant growth and development. These processes include the assimilation and distribution of amino acids in cells, the short-distance and long-distance transport of amino acids, and the absorption and utilization of amino acids (Fang et al., 2021). A large number of studies have showed that AAT is an important regulator and played a very important role in the growth and development of plant (Peng et al., 2016). At present, there is still little known about the functions of different AATs and their effects on plants.

AATs play an important role in transport process of various amino acids, and the research scope of AATs in plants is becoming wider and wider. In addition to the model plants *Arabidopsis* and rice, there are also wheat, corn, broad beans, peas, etc. (Pan et al., 2015). Among them, rice as an important food crop is more and more studied, and there are more and more studies on wheat and corn. With the cloning of AAT genes, this paper reviewed the classification and function of AAT genes that have been isolated and cloned, which could provide reference for the in-depth study of AATs in plants.

2. The Classification of AATs in Plants

A large number of studies have showed that AATs are relatively conserved in animals, plants and fungi. AAT family genes are mainly divided into two large families in plants, including AAAP (amino acid/auxin osmotic enzyme family) or ATF (amino acid transporter family) and APC (amino acid polyamine organic cation family). AAAP family includes amino acid permeable enzymes (AAPs), lysine like and histidine transporters (LHTs), proline transporters (ProTs), γ -Aminobutyric acid transporters (GATs), aromatic and neutral AATs similar to ANTI, auxin transporters (AUX); APC family includes cationic AATs (CATs), amino acid choline transporters (ACTs) and polyamine hydrogen ion Symporters (PHSs) (Dinkeloo et al., 2018). With the deepening of research, a new family of transporters has been found recently. This family is usually multiple amino acid import and export transporter (UMAMIT) (Denancé et al., 2014; Wang et al., 2018), which is part of the drug/metabolic transporter (DMT) superfamily (Whyte-Allman et al., 2020). With the increasing interest in the field of amino acid transport, the number of organisms studying amino acid transport is also increasing. Through genome-wide investigation of different species, previously unknown AATs can be more directly identified, such as rice (Zhao et al., 2012), selaginella (Yang et al., 2015), poplar (Wu et al., 2015), soybean (Lin et al., 2016), potato (Ma et al., 2016) and castor (Xie et al., 2016). Therefore, the AATs are closely related to the growth and development in plant.

With the development of genomics resources, genome-wide research has identified at least 60 AAT genes in *Arabidopsis*, 85 AAT genes in wheat, 189 AAT genes in rice, 72 AAT genes in soybean, 100 AAT genes in potato, 23 AAT genes in poplar 62 AAT genes of selaginella and 283 AAT genes of castor (Yao et al., 2020). The biochemical characteristics of these transporter genes are similar to those of *Arabidopsis*, indicating that the function of AATs is conserved in vascular plants. However, the role of each AAT in organic nitrogen distribution is far from understood. So far, the most transporters are characterized by their localization in the plasma membrane and intercellular transport, while only a few transporters transport amino acids in cells. The biological functions of AATs need to be further studied in the future.

In *Arabidopsis*, more than 60 AATs have been identified. AAP and LHT families are the most studied. The research on their specific substrates, gene localization and biological functions is more systematic, but the research on AATs in rice is less. By analysis all the possible 85 AAT genes in rice, it is found that they are distributed on 12 chromosomes of rice, and most of the AATs belong to AAAP superfamily and some belong to APC superfamily, in which many domains are relatively conserved in different AATs, in terms of evolutionary relationship, it is highly similar to *Arabidopsis*. Among these 85 genes, 47 genes had individual replication and tandem replication events in the process of evolution. Lu et al. conducted in-depth research on the AAT gene family of rice and identified 79 AAT genes, which are distributed on 11 chromosomes of rice (except chromosome 9). Cluster analysis based on its full-length protein sequence reveals that AATs in rice can be divided into four subgroups: A, B, C and D, including 8, 28, 15 and 28 AATs (Lu et al., 2012; Zhao et al., 2012). Taking the gene of rice *OsAAP1-OsAAP18* as the reference sequence, 47 genes in 21 chromosomes of wheat and 13 genes have copies in A, B and D homologous groups of wheat. Amino acid similarity comparison showed that there is high homology (> 80%) between copies. AAPs in wheat were located on the cytoplasmic membrane. Cluster analysis was carried out with *Arabidopsis*, rice, corn, two spike short stalk grass and wheat to analyze the genetic relationship of wheat AAPs family members. They were divided into two categories A and B, and can be further divided into four subclasses (A1, A2, B1 and B2). It is predicted that *TaAAP1*, *TaAAP3*, *TaAAP6*, *TaAAP7*, *TaAAP8*, *TaAAP12* and *TaAAP15* may have functions similar to known AAPs. The analysis of the biological functions of these AATs in *Arabidopsis* will provide important information for the functional study of AATs in other plants.

3. The Isolation of AATs in Plants

The large family of AATs in plants has lots of family members. In the AAAP family, most of the AAT genes isolated and cloned by molecular biological methods belong to the common amino acid permeability enzyme family (AAPs), and the research on *Arabidopsis* is the most in-depth. The AAT genes isolated from the eight members of the AAP family (*AtAAP1-AtAAP8*) are *AtAAP1*, *AtAAP2*, *AtAAP3*, *AtAAP5*, *AtAAP6*, *AtAAP7* and

AtAAP8. At present, *OsAAP1*, *OsAAP3*, *OsAAP4*, *OsAAP5* and *OsAAP6* have been isolated and cloned from 19 kinds of AAP transporters in rice. In addition to *Arabidopsis* and rice, it has also been studied in other plants, such as *VfAAP1*, *VfAAP3*, *StAAP1*, *PvAAP1*, *PtAAP11*, *PsAAP1*, *PsAAP6*, *TaAAP1*, *TaAAP3*, *TaAAP6*, *TaAAP7*, *TaAAP8*, *TaAAP12*, *TaAAP15*, *CsAAP3*, *CsAAP4*, *CsAAP6*, *CsAAP7*, *CsAAP8* and *ZmAAP4*. The isolation and cloning of AAT gene function in plants have provided an important reference for the study of the AATs in rice and other major food crops.

The amino acid transporter genes isolated and cloned in *Arabidopsis* are *AtLHT1* and *AtLHT2*. *AtLHT4*, *AtLHT5* and *AtLHT6* are also reported in the literature. *OsLHT1* and *OsLHT6* have been isolated and cloned from rice. *CsLHT1*, *CsLHT2*, *CsLHT6*, *CsLHT8.1* and *CsLHT8.2* were reported in tea plants. The other four subfamily genes except *CsLHT2* were successfully cloned. GAT subfamily mainly transports GABA (γ -Aminobutyric acid) and GABA related compounds have high affinity for GABA transport. In the GAT subfamily, the isolated and cloned AAT gene is *AtGAT1*. High affinity of AUX subfamily mediates the transport of indoleacetic acid (IAA). The AAT genes isolated and cloned in AUX subfamily include *AtAUX1*, *OsAUX1*, *AtAUX3* and *AtAUX4*. *AtAUX2* and *AtAUX5* have been reported in the literature. Proline transporters (ProTs) subfamily members have similar substrate specificity, mainly mediating proline, betaine and γ -Aminobutyric acid transport and other compounds, *StProT3* has been isolated and cloned, and *AtProT1*, *AtProT2*, *AtProT3*, *HvProT2*, *GmProT1* and *GmProT2* have been reported in the literature^[2]. However, in the APC family, there are few isolated and cloned AAT genes, which can be roughly divided into two categories. At present, the isolated and cloned AAT genes are *AtCAT1* and *AtCAT2*, and the literature reports are *AtCAT3-AtCAT9*, *PtCAT11* and *SiCAT2*. In addition, *AtLAT1*, *AtLAT4* and *AtLAT5* have also been cloned.

Amino acids are important not only to the synthesis of proteins or various enzymes, but also are the precursors of many key compounds (phytohormones and signaling molecules, etc.), such as some compounds that play important roles in the growth, development, metabolism and defense of organisms. At present, the cloning and isolation of AATs are mostly started from the two species of *Arabidopsis* and rice. Because the amino acid osmotic enzyme family is highly consistent with *Arabidopsis* in evolution and may have some similarities in function, a large number of AATs in other plants have been cloned and analyzed. It not only provides a favorable support for further study of gene function, but also lays a foundation for cloning new genes in rice.

4. The Function of the AATs in Plants

At present, studies on the regulation of AATs expression are mainly focused on the transcriptional level, and there is no experimental evidence to support that post-transcriptional regulation of AATs exists in plants or AATs are controlled by post-transcriptional modification. AATs are a kind of membrane proteins that can mediate the transmembrane transport of amino acids. They play an indispensable role in all processes of plant growth and development. Including long-distance transport of amino acids, response to pathogens, abiotic stress, assimilation and distribution of amino acids in cells, short-distance and long-distance transport of amino acids, and absorption and utilization of amino acids by library organs (Yang et al., 2020; Tegeder et al., 2012; Besnard et al., 2021; Garneau et al., 2018). The research on the function and mechanism of plant AAPs mainly focuses on the model plants *Arabidopsis thaliana* and *Oryza sativa*. Through the functional research of AAT genes by means of amino acid uptake test, field culture and subcellular localization, it is found that most of the amino acid permeability enzyme families are located on the plasma membrane, *AtAAP1* gene is mainly expressed in leaves and endosperm. It is also involved in the transport of amino acids to roots and embryos. *AtAAP5* gene mainly plays an important role in the process of roots absorbing amino acids in soil. It may also be involved in the process of transporting amino acids to embryos. *AtAAP6* gene plays an important role in regulating the composition of molecular sieve. *AtAAP7* and *AtAAP8* have the highest expression levels in stems and roots, *AtAAP8* gene may be involved in the transport of amino acids to endosperm and seeds during the early development of *Arabidopsis* seeds. In *Arabidopsis*, eight AAP transporters (*AtAAP1-AtAAP8*) play an important role in amino acid transport of organic nitrogen utilization in source and sink organs (Chen et al., 2021). For example, *AtAAP2* has been found to transport glutamate and neutral amino acids and plays an important role in the transport of amino acids from xylem to phloem. In addition, *AtAAP3* mediates the uptake of neutral and basic amino acids, *AtAAP4* mediates neutral amino acids Pro and Val (Ren et al., 2019), and *AtAAP8* plays an important role in the entry of neutral and acidic amino acids into phloem and the distribution of nitrogen. The cloning and functional analysis of AAT genes is most deeply studied in *A. thaliana*. Among the 8 members of AAP family (*AtAAP1-AtAAP8*), *AtAAP3* and *AtAAP5* proteins can transport acidic, neutral and basic amino acids, while other 6 members can generally transport neutral and acidic amino acids.

However, there are more AAP genes in rice and other monocotyledonous plants than in *Arabidopsis*. Therefore, even if the function of AAPs in *Arabidopsis* has been studied, it is also important to directly analyze the function

of monocotyledon AAPs. At present, *OsAAP1*, *OsAAP3*, *OsAAP4*, *OsAAP5* and *OsAAP6* have been isolated and cloned in rice. Among the 19 transport genes in rice, *OsAAP6* is reported to affect the distribution of various amino acids in plants and act as a positive regulator of rice protein content and rice quality (Peng et al., 2014). *OsAAP3* can transport Ala, Leu and Met, indicating that *OsAAP3* mainly transports basic amino acids Lys and Arg and has selectivity for aromatic amino acids (Taylor et al., 2015). In recent studies, blocking the expression of *OsAAP3* or *OsAAP5* can improve grain yield by adjusting the concentration of these two amino acids (Lu et al., 2018; Wang et al., 2019). Some experiments have interfered with rice plants through *OsAAP5* gene. It is found that reducing *OsAAP5* gene expression can increase the normal rice root length, root number, plant height and fresh weight. Therefore, *OsAAP5* gene can be used in rice breeding to promote rice growth and improve rice biomass. *OsAAP5* gene has important application Val in explaining the influence of amino acid transport on plant growth and development. In addition, the amino acid transporter *OsAAP1* regulates growth and grain yield by regulating the absorption and redistribution of neutral amino acids in rice (Ji et al., 2020). *OsAAP7* and *OsAAP16* belong to specific branches of monocotyledons, but their substrate specificity is very similar to *OsAAP1*, except that *OsAAP7* and *OsAAP16* transport arginine to a greater extent than *OsAAP1* (Taylor et al., 2015). Recent studies have found that the amino acid transporter *OsAAP4* positively regulates rice tillering and yield by regulating the distribution of neutral amino acids through two different splicing variants, and found that different variants have different effects on agronomic characters under different amino acid concentrations. Through overexpression of *OsAAP4* gene, it is found that increasing the expression of *OsAAP4* gene can increase the number of tillers and panicles per plant. Therefore, *OsAAP4* gene can be used in rice breeding to improve rice yield (Fang et al., 2021). *OsAAP7*, *OsAAP8*, *OsAAP15* and *OsAAP16* all showed similar expression patterns in the development process of rice and resistance to abiotic stress, indicating that the functions of these genes may be redundant. Therefore, the transporter genes of amino acid permeability enzyme family are mainly used to transport amino acids in *Arabidopsis* by affecting the uptake of amino acids, and the AATs are also involved in the regulation of rice yield traits.

VfAAP1 and *VfAAP3* in broad bean transport a wide range of amino acids, in which *VfAAP1* prefers Cys and *VfAAP3* prefers Lys and Arg. *StAAP1* in potato is expressed in mature leaves. Antisense inhibition of this gene can reduce the amino acid content of transgenic potato. *PvAAP1* is expressed in epidermal cells, xylem parenchyma cells and phloem of *Phaseolus vulgaris*, and participates in xylem phloem transfer and phloem loading to transport amino acids to sink tissue. In addition, it is also proposed that *PtAAP11* provides Pro and plays a major role in the formation of xylem of *Populus tomentosa*. Recently, it has been found that the overexpression of *PsAAP1* positively regulates the amino acid transport of pea from source organ to sink organ, and affects the nitrogen utilization efficiency of plants. *PsAAP6* plays a role in nitrogen metabolism, output and plant nutrition of root nodules (Perchilk et al., 2017; Garneau et al., 2018). *ZmAAP4* in maize is a broad-spectrum AAT with different substrate selectivity and transport capacity (Pan et al., 2015). The cloning of *TαAAP6* in wheat found that the gene may play a role in resisting abiotic stress, which provides a certain theoretical basis and candidate gene resources for wheat quality (Jin et al., 2018). The expression of subfamily genes of AATs in tea plants is also affected by nitrogen level and variety genotype.

In *Arabidopsis*, the *AtLHT1* transporter can promote the uptake and transport of Glycine clofenidine conjugate in *Arabidopsis* (Chen et al., 2018). The expression of *AtLHT2* is organ specific and a transport system with high affinity for acidic and neutral amino acids (Wang et al., 2019). The expression of LHT amino acid transporter is mainly strongly expressed in flowers. The study on the promoter GUS in *AtLHT2*, *AtLHT4*, *AtLHT5* and *AtLHT6* found that GUS staining depends on the transporter and is located in the tapetum cells of anthers, germinating pollen, pollen tube, stigma or pistil. Subcellular localization showed that all LHT transporters targeted the plasma membrane (Gratz et al., 2021). However, in rice, through genome-wide association analysis of aspartic acid absorption of 68 rice varieties, *OsLHT1* was determined to be the main candidate for aspartic acid acquisition by rice roots. In addition, the growth and absorption of amino acids and NH_4^+ of *OsLHT1* mutant were studied. It was found that the function of *OsLHT1* affects root growth and is involved in the absorption of amino acids and amides from soil. Analysis of nitrogen levels in xylem and shoot of *OsLHT1* mutant treated with NH_4^+ showed that *OsLHT1* mutant also affected the supply of amino acids from root to shoot (Guo et al., 2020). It has been reported that *OsLHT6* is specifically expressed in shoot meristem (Liu et al., 2018). It can be seen that LHT subfamily also plays a very important role in amino acid transport, and the research is more comprehensive in *Arabidopsis*.

The analysis of substrate selectivity and kinetic characteristics shows that *AtGAT1* mediated transport is similar to but different from that of mammals, bacteria and *Saccharomyces cerevisiae*. In AUX subfamily, *AtAUX1* has the highest expression in plant flowers and also plays a role in leaf development. Similarly, its homologous gene

SILAX1 has been found in tomato to control leaf development (Imriani et al., 2018). *AtLAX3* is mainly expressed in roots and promotes lateral root formation. *OsAUX1* controls primary root elongation (Chen et al., 2020), *OsAUX3* module regulates rice grain length and weight (Qiao et al., 2021), *OsAUX4* is widely expressed in roots and located on the plasma membrane, which may play a role in the regulation of root development (Ye et al., 2021). In the ProTs subfamily, the isolated *StProT3* gene is involved in hormone signal transduction and abiotic stress response of potato (Wang et al., 2021). It can be seen that the AAT genes of GAT subfamily and ProTs subfamily not only transport amino acids, but also play a certain role in plants development and response to environmental signals. In the GAT subfamily, *AtGATI* has no sequence similarity with any no plant GABA transporters described so far. In APC family, *AtCAT1* has high affinity for basic amino acids and low affinity for neutral or acidic amino acids in amino acid transport, *AtCAT2* is mainly used to maintain the steady state of amino acid concentration in the environment (Yang et al., 2014), *AtCAT3*, *AtCAT6* and *AtCAT8* are mainly involved in the transport of neutral or acidic amino acids, *AtCAT5* high affinity mediates the transport of basic amino acids, which may be involved in the absorption and utilization of amino acids in leaf margin leakage, *AtCAT8* mainly mediates the absorption of glutamate and glutamine and distributes them to the young meristem. *AtCAT9* affects plant nitrogen storage, reuse and intracellular amino acid homeostasis. *PtCAT11* is highly expressed in the aging stage and promotes nitrogen reuse by promoting the loading of Glu in phloem. *SICAT2* is the first vacuolar transport or efflux transporter with acetylcholine as substrate, but *SICAT2* has more affinity for Arg, indicating that *SICAT2* may transport arginine mainly through the way of cross vacuolar membrane (Liu et al., 2018). There are relatively few studies on AAT genes in APC family.

5. The Application of AATs in Plants

In recent years, the regulation, perception and signal transduction mechanisms of amino acid transport have been discussed. The studies include the regulation of a variety of enzymes and transporters, because the enzymes involved in amino acid biosynthesis are regulated by biological and abiotic stresses. Environmental signals, such as nutrition, light, salt and drought stress and the attack of nematodes or pathogens, can also affect the expression of AATs (Peatelli et al., 2014; Yao et al., 2020). At present, the research on basic acid transporters is mainly limited to model plants such as *Arabidopsis*, rice and pea, and less in other species, especially economic crops, or only limited to a few transporter families, gene function, molecular regulation mechanism of plant AAT family, and interaction with nitrogen nutrient efficiency and nutrient elements. The relationship between plant yield, quality, disease resistance and AAT is still the focus of future research. Amino acid transporter is the main medium of nitrogen distribution in plants, which is very important to maintain the growth and development in plants. The mining and analysis of AAT gene function provides important information for the genetic improvement of the yield and quality traits in plants.

In plants, AATs are a kind of membrane proteins that can mediate amino acid transmembrane transport and play an indispensable role in various processes of growth and development (Peng et al., 2018), including long-distance transport of amino acids, seed loading, response to pathogens and abiotic stress (Yang et al., 2021). About 65% of the global edible protein provided for human nutrition comes from plants. Thus, the content of protein and amino acids is the key factor to determine the nutritional quality of seeds. Generally speaking, all amino acids are transported to seeds through phloem and then used for protein synthesis (Chen et al., 2013; Kong et al., 2018; Wang et al., 2015; Wang et al., 2015; Wei et al., 2017). Moreover, with the continuous development of the times, people's demand for high nutritional quality crops continue to increased (Zeng et al., 2017; Das et al., 2020). Therefore, it is of great significance to make full use of the effects of amino acids on plant growth and development to improve the protein content and nutritional quality of crops in the future breeding research of rice, corn, wheat and other crops. With the rapid development of biotechnology and functional genome, more and more AAT genes have been isolated and cloned in model plants. These AAT genes will provide important gene resources for the genetic improvement of the yield and quality traits in plants, and may provide new genes for the cultivation of new varieties in major food crops.

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