Bio-synthetic pathway of trehalose and its response to plant stress

Yao Chen [1], **Cuiling Tong** [2], **Dejian Zhang** [3*]

[1, 3] College of Horticulture and Gardening, Yangtze University, Jingzhou 434025, Hubei, China

[2] Jingzhou Institute of Technology, Jingzhou, Hubei, China

* Corresponding Author: **Dejian Zhang**

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Abstract

Trehalose is a non-reducing disaccharide that is widely found in living organisms and consists of two glucose residues bound by an α-α- (1→1) bond that serves as an energy source, penetrant, and protein/membrane protector. Trehalose, as a relatively low content of metabolic substances, exists for a long time, helps plants resist the stress of adversity, and plays an irreplaceable protective role for plants. In this paper, the bio-synthetic pathway of trehalose, its response to stress and the molecular mechanism of regulation were summarized in order to provide reference for improving plant stress resistance by trehalose.

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1. Introduction

Trehalose (Tre) is a non-reducing disaccharide that is widely found in bacteria, fungi and plants [1]. Tre content in plants is generally low, more as a signaling molecule. Trehalose is very stable and can maintain membrane structure and protein stability under high temperature, cold, high osmotic pressure and dehydration, and plays a very important role in plant growth [2]. When plants are in the growth period, trehalose ‘hibernates’ in the plant body to supply energy for them, while in the face of adversity stress, trehalose, as a relatively low content of metabolic substances, exists for a long time to help plants resist the stress of adversity, and plays an irreplaceable protective role for plants.

2. Biosynthetic pathway of trehalose

Five pathways of trehalose biosynthesis have been identified.

2.1 The most widely distributed pathway is the Ots A-Ots B pathway, which is found in archaea, bacteria, fungi, plants, arthropods, Trehalose-6-phosphate synthase (TPS) catalyzes the transfer of glucose groups from uridine glucose diphosphate (UDP-Glc) to glucose 6-phosphate (Glc-6-P) to produce trehalose 6-phosphate (T6P). Later, T6P is dephosphorylated to produce trehalose by Trehalose-6-phosphate phosphatase (TPP) [3].

2.2 The Tre P pathway has been found in the trehalose phosphorylase (Tre P), which catalyzes glucose-1-phosphoric acid and glucose to produce trehalose [4].

2.3 The Tre S pathway was found in bacteria, where maltose underwent intramolecular recombination isomerization to form trehalose under the catalysis of trehalose synthase (Tre S) [5].

2.4 A trehalogenesis pathway named trehalose Tre -Tre Z was discovered in paleontobacter. maltooligosyl trehalose synthase (Tre Y) was used to catalyze the formation of maltooligosaccharide trehalose using maltodextrin as a substrate. It was hydrolyzed to trehalose by maltooligosyl trehalose trehalohydrolase (Tre Z) [6].

2.5 The Tret pathway is found in *Thermococcus litoralis*, which is catalyzed to trehalose adenosine diphosphate by trehalose glycosyltransferring synthase (Tre T) using ADP-glucose and glucose molecules as substrates [7].

3. Trehalose is involved in plant response to stress

It has been reported that trehalose plays an important role in plant growth, development and resistance to stress. Trehalose acts as the primary osmoprotector to protect proteins and cell membranes during dehydration in folding leaf, *Selaginella* and *Selaginella squamata*, and these dehydrating tolerant plants can withstand almost complete dehydration and recover full viability after rehydration. Studies have found that *Selaginella* can reduce its metabolism and accumulate large amounts of trehalose in the body, thereby enhancing its ability to survive in drought conditions [8]. Studies have shown that the trehalose level of *Arabidopsis thaliana* is doubled after heat shock treatment. After four days of cold treatment, trehalose levels increased eight-fold. The contents of soluble sugar in cassava were analyzed. It was found that sucrose, fructose and so on had low water retention ability, while trehalose played an important role in cassava under dehydration stress. It was found that under high temperature stress, exogenous trehalose can enhance the antioxidant system of *Paeonia lactis*, protect the integrity of cells, and induce the expression of genes related to high temperature tolerance to varying degrees, effectively alleviating the damage caused by high temperature. Under nitrogen deficiency conditions, trehalose treatment increased chlorophyll content, total nitrogen content and photosynthetic rate of tobacco leaves, and the total biomass accumulation was higher, partially alleviating the symptoms of nitrogen deficiency. Under drought conditions, trehalose spray on maize leaves can significantly increase plant biomass, enhance the regulation of photosynthesis, osmotic potential and active oxygen scavenging enzymes, and significantly improve the drought resistance of plants. Trehalose can also alleviate the inhibitory effect of salt stress on the biomass and flowers of *Arabidopsis thaliana*, regulate the REDOX state of cells, reduce the accumulation of ROS, reduce salt-induced cell death, and increase the enzyme activity and soluble sugar content of the antioxidant system, thus improving the salt tolerance of *Arabidopsis thaliana*.

4. Molecular mechanism of trehalose involved in plant stress

Previous studies have shown that trehalose can help plants withstand harsh living conditions, even when the temperature difference is large, the soil salt is high, the climate is relatively dry or low nitrogen environment can grow well. Exogenous trehalose can protect plants from damage caused by high temperature. Trehalose treatment can improve the maximum optical efficiency and electron transfer rate of PSII of wheat seedlings after heat stress recovery, and dry mass and leaf water content of plants after normal recovery can be improved to a certain extent. Intracellular protection of PSII under stress was achieved through the increase of proton gradient and ATP synthase activity in thylakoid membrane. In addition, trehalose pre-treatment can reduce the inhibition effect of high temperature and drought stress on the plastiquinone pool, and alleviate the photo inhibition of plants under abiotic stress by circulating electron flow and plastiquinone pool. In addition, trehalose treatment regulates antioxidant enzyme activity and osmotic balance, The expression levels of antioxidant genes (*CAT12*, *POD34* and *FSD7*), cold stress response marker genes (*CBF1*, *CBF2*, *CBF4*, *COR6.6*, *COR15*, *COR25*, *COL1* and *KIN1*) and trehalosaccharide biosynthesis genes (*TPS4*, *TPS8* and *TPS9*) were increased. The adverse effects of cold stress on rapeseed seedlings were alleviated and the survival rate of seedlings under cold stress was increased [9].

5. Signal transduction of trehalose

Trehalose phosphate synthase (TPS) and trehalose phosphate phosphatase (TPP) participate in the synthesis of Tre, while trehalose decomposes Tre into Glc. The *Arabidopsis* genome contains 11 *TPS* genes, 10 *TPP* genes and 1 trehalase gene [10]. *Arabidopsis TPS1* integrates carbon and nitrogen signals, regulates NADPH production and nitrate reductase activity. It is worth noting that the *TPS1* gene is necessary for embryonic development, because the *tps1* mutant is embryo-lethal. *TPS1* also regulates flower development. Allogenic expression of *TPS1* promotes the branching of inflorescence. tps1 phenotype can be restored by T6P application, but not by Tre application.

The synthesis of T6P reflects the availability of hexose phosphate, UDPG and Suc in plant cells, so T6P can be used as a signaling molecule to regulate plant growth and development. T6P regulates the utilization of sucrose, and its content is affected by sucrose. T6P activates AGPase, the key enzyme of starch synthesis, and promotes starch synthesis. In addition, ABI4 accelerates the breakdown of Tre by promoting β-amylase gene transcription. Biochemical experiments showed that it was T6P but not other sugars that inhibited *SnRK1* kinase activity in *Arabidopsis*. *WRI1*, a high concentration of sucrose stable transcription factor, promoted fatty acid synthesis, and T6P promoted fatty acid synthesis.

Tre is involved in responding to plant nutrient stress. Tre application can increase nitrate and ammonia assimilation in tobacco leaves, improve the activities of nitrate reductase, glutamine synthetase and glutaminoxy-glutarate aminotransferase, positively regulate nitrogen metabolism, and alleviate the symptoms of nitrogen deficiency in tobacco to a certain extent. Under the condition of sufficient nitrogen, the effect of Tre is very small.

Exogenous abiotic stress produces stress resistance through activation of Tre related synthetic genes. Rice transcription factor OsbHLH002/OsICE1 is phosphorylated by *OsMAPK3* under low temperature stress, resulting in the accumulation of phosphorylated OsICE1, which can directly promote the expression of the key enzyme gene encoding trehalose biosynthesis (*OsTPP1*), increase Tre content and improve cold resistance.

Tre regulates plant stress resistance by participating in other sugar signaling. *AtTPPD*, a member of the TPP family in *Arabidopsis thaliana*, is an enzyme localized to chloroplasts. Plants lacking *AtTPPD* were sensitive to high salt stress, while plants overexpressing *AtTPPD* showed stronger tolerance to high salt stress due to increased starch levels and soluble sugar accumulation, indicating that *AtTPPD* regulates glucose metabolism under salt stress.

6. Looking forward

With the deepening of plant trehalose research, its physiological function and mechanism of regulating plant growth and development have been gradually revealed. However, compared with traditional crops, the studies on the regulation of trehalose on the growth and development and stress resistance of cash crops are still very limited, and there are still some problems that need to be further explored and solved. In addition, there is a complex trehalose signal transduction system in plants, and trehalose regulates gene expression at the transcriptional and post-transcriptional levels, thereby regulating plant growth, development and related metabolism. Current studies on trehalose related genes (proteins) are not systematic and comprehensive. In the future, molecular biology and genetics research techniques should be more widely applied to explore the signal transduction mechanism of trehalose, deeply reveal the relationship between different trehalose signal transduction and regulatory gene expression, and analyze whether different plants have the same trehalose signal transduction pathway.

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Conclusion

Trehalose plays a vital role in plant growth, development, and stress resistance. It acts as an osmoprotector, aiding dehydration-tolerant plants like Selaginella to survive extreme dehydration. Studies show that trehalose levels increase under heat, cold, and drought stress, enhancing plants' resilience. Exogenous trehalose improves antioxidant systems, osmotic balance, and stress-related gene expression, aiding plants like maize, cassava, and tobacco. The trehalose biosynthesis and signaling pathways involve key enzymes and genes that regulate plant responses to nutrient and abiotic stresses. Future research should focus on the trehalose signal transduction system and its role in different plants.

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