

海藻糖介导的信号转导与植物抗逆性

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摘要:海藻糖是一种非还原性二糖, 它广泛存在于细菌、真菌、酵母、昆虫、无脊椎动物和植物等生物体内。海藻糖不仅作为碳水化合物化合物的储备, 而且还是一个多功能分子。海藻糖作为一种信号分子, 启动信号转导级联反应, 改变基因表达和酶的活性, 与激素也有一定的关系。采用基因工程和通过外源施加的方法增加海藻糖在植物体内的积累可以提高植物的抗逆性, 这为提高农作物的抗逆性提供了新的策略。

关键词:海藻糖; 信号转导; 植物; 抗逆性

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Trehalose-mediated signal transduction and stress tolerance in plants

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Abstract: Trehalose is a non-reducing disaccharide widespread in organisms, including bacteria, fungi, yeast, insects, invertebrates and plants. It is not only a carbohydrate reservoir but also a multifunctional molecule. Trehalose, which have some connections with hormones, too, has been recognized as a signaling molecule to initiate signal transduction cascades that result in a series of cellular responses such as altering gene expression and enzymatic activities. Increasing the accumulation of trehalose in plants by both gene engineering and exogenously supplied trehalose can improve stress tolerance of plants, this offers a novel strategy for improving stress tolerance in crop plants. This article reviews the current achievements in trehalose-mediated signal transduction.

Key Words: trehalose; signal transduction; high plants; stress tolerance

Trehalose (α -D-glucopyranosyl-[1, 1]- α -D-glucopyranoside) is a non-reducing disaccharide that is consisted of two glucose units joined by an α , α -1, 1 linkage, and was thought to be absent from all but a few highly desiccation-tolerant plants, such as *Selaginella lepidophylla* and *Myrothamnus flabelifolius*^[1]. However, with the

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identification of trehalose in potato^[2] and the continual find of genes related with trehalose metabolism in some high plants such as *Arabidopsis*^[3], in the present, it is considered that trehalose is widespread in living organisms and recognized universally as a crucial defense mechanism that stabilizes proteins and biological membranes under a variety of adverse conditions^[4-8]. Some reviews have been given about its metabolism, functions and productive approaches^[9-11]. Alternatively, trehalose has been accepted as a signaling molecule^[12,13] and the interest in it has been increased accordingly. This article provides a comprehensive review of the current achievements in the signal transduction of trehalose and the connection between trehalose and hormones, and presents a hypothesis to improve stress tolerance of plants through trehalose signal finally.

1 Trehalose Signal and Its Possible Signal Transduction Pathways

In the past, sugars were long believed to be substrates for respiration, metabolic intermediates and carbohydrate reservoir, and their effects on gene expression, plant growth and development were often attributed to their metabolism and energy, but not thought of as signals. However, more and more studies have shown that sugars are also signaling molecules recently, besides, sugar sensing and signal transduction are not coupled up with sugar metabolism^[14-16]. Sugar sensing can be defined as the interaction between a sugar molecule and a sensor protein, in such way as a signal is generated. This signal can initiate signal transduction cascades that result in a series of cellular responses such as altering gene expression and enzymatic activities.

1.1 Possible Sugar Sensing Paths in Plants

There might be four paths of sugar sensing in plants, which are (a) hexokinase (HXK)-linked sensing, (b) membrane sensor-based sensing, (c) acetate and/or respiratory metabolites-involved sensing, and (d) other signals and/or crosstalk^[17,18]. HXK is a hexose sensor protein and hexose phosphorylation by HXK is an important sugar sensing mechanism in yeast and animal systems. But, the function of HXK as a hexose sensor in plants has not been generally accepted^[19,20]. Trehalose-6-phosphate (T6P), the precursor of trehalose is a strong inhibitor of hexokinase II (HXK II), an isoform of hexokinase, at physiological concentrations^[21]. This inhibition may be caused by the competition between trehalose and the precursor of HXK II or by the suppression of gene expression related to composing HXK II. It is possible that different HXK isoforms and HXK-like proteins have different metabolic and signaling functions and sugars may be sensed at the plasma membrane by sugar transporters or transporter-like proteins or by specific sugar receptors. Unfortunately, it has not been found how trehalose is sensed till now.

1.2 Trehalose Itself as A Signal

As for trehalose signal, it was first brought forward that trehalose metabolism performed a signaling role in yeast and it was implicated in the control of glycolytic flux and sugar signaling^[12]. In plants, maybe, trehalose has the same signaling function. The research in *Arabidopsis* plants by Müller *et al.* showed that both the inhibition of trehalase by validamycin A (a specific inhibitor of trehalase) and exogenously fed trehalose led to an alteration in carbohydrate pool sizes^[14]. In addition, overexpression of *Escherichia coli* trehalose biosynthetic genes in rice increased trehalose accumulation which correlated with higher soluble carbohydrate levels^[15], suggesting that trehalose or trehalose metabolites are signals in carbohydrate metabolism or allocation in plants.

It has been known that nearly all of the transgenic plants expressing trehalose metabolism- relevant genes showed some changed phenotypes, including stunted growth, inhibited leaf expansion and disturbed root system^[22-25]. We also noticed that, trehalose exogenously supplied in winter wheat could increase the accumulation of trehalose, but root elongation was inhibited (data will be published). These abnormal phenotypes, might be due to the following reasons: 1) trehalose interfering with the normal plant metabolism such as photosynthesis and carbohydrate metabolism^[26-28]. But, others argue that the precursor of trehalose, trehalose-6-phosphate (T6P) is a regulatory

molecule involved in control of carbon metabolism in connection with growth and development^[29-31]. 2) trehalose metabolism acting as a signal in sugar sensing and partitioning of assimilation^[16]. Besides, it might suggest that as a signal, trehalose performs function in isolation or combined with other signal transduction pathways through cross-talk, which often activates a much wider network of genes including some incorrect genes. Such, over activation or incorrect gene expression of trehalose metabolism may influence hexose or redox signaling which is important in long-range transmission throughout the whole plant and then result in deleterious effects on total plant performance. Maybe trehalose plays a part in systemic signaling, too^[32]. In addition, whether the way of trehalose transport is different between subcellular compartments and different organs or not, which contributes to these pleiotropic effects, still has been unknown. In fact, when engineering other sugars, like sorbitol, abnormal phenotypes occurred, too^[33]. This adverse influence seems to be common in sugars. In this review, we emphasize the role of trehalose as a signal.

As a signal, since trehalose could affect carbohydrate-mediated gene expression, then, how it is sensed? Two hypothetical mechanisms could be suggested: trehalose itself or the catabolites of trehalose as signals.

As an analogue of sucrose or after cleavage by release of glucose, trehalose plays a role in metabolic fine-tuning and, ultimately, in plant development. But more experiments supported the former one. First, trehalose, glucose and fructose all can enhance the activity of sucrose:fructan-6-fructosyltransferase (an enzyme catalyzing fructan biosynthesis), but the inductive ability of trehalose is the highest of all^[34], which indicates that trehalose sensing does not depend on hexose sensing, namely, it is impossible for trehalose to function only after it is degraded into glucose. Second, trehalose can induce the production of sucrose synthase and it also has this stimulatory effect in the presence of the trehalase inhibitor validamycin A^[26], suggesting that this induction is also due to trehalose itself (or a derivative) rather than trehalose degradation. Most recently, Kolbe *et al.* have shown that trehalose feeding to potato tubers and *Arabidopsis* leaves increased reductive activation of AGPase and starch synthesis, but did not change hexose-phosphate levels or NADPH/NADP⁺ ratio in the tissue^[16]. This response resembled sucrose feeding but was opposite to glucose feeding^[35]. Hence, it should be possible that it is trehalose itself plays a key role, but not glucose, the product of its metabolism.

1.3 Possible Signal Transduction Pathways as That of Sucrose

The signaling function for sucrose has long been accepted. In experiments with excised sugar beet leaves, sucrose repressed mRNA levels and transport activity of the proton-sucrose symporter, while glucose and fructose, the metabolic production of sucrose had no effect on it, suggesting sucrose is a signal molecule in assimilate partitioning^[36]. Metabolizable and non-metabolizable sugars also have different signal transduction pathways. Metabolizable sugars such as sucrose, in general, seem to repress photosynthetic genes, whereas sink-specific enzymes are induced^[37]. Then, if trehalose is a signal as the same or similar signal transduction pathways as that of sucrose, what relationship between both sugar species does there exist? Fortunately, it was reported that trehalose addition to soybean induced sucrose synthase and alkaline invertase activity^[26], both of which are enzymes decomposing sucrose. Moreover, Trehalose has the same transport system as that of sucrose^[38]. Therefore, if the relationship between both sugars is simplified, it is possible that trehalose performs function to influence plant growth through sucrose or they activate the same reactive molecule. However, the detailed mechanism, including the node between both sugars, is not clear yet. Recently, a trehalose receptor gene has been cloned from fruit-fly (*Drosophila*)^[39]. Meanwhile, it is reported that the trehalose receptor in mammals is formed by combining a part of the receptor of sucrose with a G protein α -subunit (<http://www.freshpatents.com>). Whether the receptor in plants is the same as that in mammals needs further researches.

Except for that above, similar to sucrose, trehalose induces the activity of enzymes involved in the accumulation

of storage carbohydrates in photosynthetic tissues, for example, in barley, exogenously supplied trehalose induces the activity of sucrose: fructan-6- fructosyltransferase^[34], which maybe related with trehalose signal.

In a word, trehalose can influence carbohydrate allocation in plants and may work through sucrose or may have the same or similar signal transduction pathway as that of sucrose. The activated sugar sensors initiate a signal transduction cascade resulting in a response such as altered gene expression, but current evidence about the signaling cascades is fragmentary. To date, we only know that protein phosphorylation and dephosphorylation, Ca^{2+} , and calmodulin (CaM) are involved in this signaling cascade^[40-42]. And we even know little about the exact trehalose-mediated signaling pathway.

2 The Connection between Trehalose and Hormones

Both sugars and hormones are signal molecules and intermediate metabolites. There are most possible that sugars have similar effects on the plant development and gene expression to phytohormones in a manner. Recently, it has been shown that they have cross talk in signal transduction and sugar-signaling pathway is subject to hormone regulation^[43]. In fact, sugar-mediated pathways do not operate in isolation but are part of cellular signal transduction networks and are linked to other signaling pathways, most notably those of hormones^[44]. One of the most common methods to unraveling the identity of signals in the interaction between sugar and plant hormones is the analysis of mutants. Using this approach, great progress has been made in the study of interplay between sugar and hormones.

There is a close interaction between sugar sensing and ethylene (ETH)-mediated signaling pathways. The *Arabidopsis* mutant *gin1* that is glucose insensitive had an impaired glucose repression of cotyledon greening and expansion, shoot development, floral transition and gene expression. This phenotype could be phenocopied in the presence of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC). Therefore, *GIN1* may act downstream of the glucose sensor and ethylene receptor. The glucose and the ethylene signaling pathways may thus converge and *GIN1* may balance the opposing roles that glucose and ethylene play in controlling developmental processes of the plant^[45].

In the mean time, by virtue of the observed phenotype defects of *Arabidopsis glucose insensitive2* (*gin2*) mutants, the links, such as auxin, gibberellins (GA) and cytokinin (CTK), have been shown between glucose signaling and plant hormones^[43]. Trehalase activity is stimulated in sterile roots upon treatment with auxin^[46], which indicates that auxin negatively correlates with trehalose content. Thus, if trehalose and auxin are concerned only, the stunted growth caused by the accumulation of trehalose may result from the decrease of auxin. Recent research has also suggested the connection between glucose and auxin, ETH or CTK signaling. Both ETH and CTK antagonize glucose signaling, and they acted independently in glucose responses, although CTK can promote ethylene biosynthesis^[43]. As for the interaction between glucose and auxin, either auxin promotes growth or inhibits growth depends on the tissue and/or glucose concentration^[43].

Absciscic acid (ABA) and two ABA-sensing proteins, ABI4 and ABI5, are now thought to be involved in the co-ordinate sensing of sucrose and glucose^[20, 47]. It was reported that ABI4 level was down-regulated in the *Arabidopsis* seedlings overexpressing trehalose-6-P (T6P) synthase *AtTPS1*, which exhibited ABA insensitive phenotypes, suggesting that trehalose metabolism was concerned with the regulation of ABA signaling during vegetative development^[31]. Whether these proteins are directly involved in the sugar signal transduction network or they are indirectly involved in regulating the responses of plant tissues to sugars is still a subject of debate. But the intact ABA signal transduction chain is important for hexokinase-dependent glucose signaling. Sugars and ABA activate "sink-related" genes such as the sporamin and β -amylase genes of sweet potato^[48]. Moreover, sugars and ABA promote tuber development^[49]. In both cases, GA has the opposite effect. ABA inhibits phloem loading of

sucrose, whereas GA promotes export of assimilates^[50,51]. Thus the ABA/GA balance may regulate cellular sugar levels. The opposite biological effect observed for ABA and GA may be due to interacting signal transduction pathways (for details to see reference 20).

The information about the connection between trehalose and hormones is insufficient, but it may be implied from that of other sugars and hormones else.

3 The Possibility of Improving Stress Tolerance through Trehalose Signal

As a compatible solute, trehalose accumulation is recognized universally as a crucial defense mechanism that stabilizes proteins and biological membranes under a variety of adverse conditions^[4-8]. In deed, trehalose appears to be superior to other sugars at conferring protection since it has a larger hydrated volume and possesses the unique feature of reversible water-absorption capacity to protect biological molecules from desiccation-induced damage. This has been proved by evidence that among some carbohydrates such as maltose, sucrose and glucose, trehalose is the most effective protectant of both proteins and membranes^[5, 52]. In addition, some researches have shown that trehalose can improve stress tolerance of plants by exogenously application or by overexpression of trehalose biosynthetic genes or by suppressed expression of genes encoding trehalase which analyzes trehalose^[14,24,25,53-57]. But the primary effect of trehalose can not be as a compatible solute because of its low accumulated level^[15]. Furthermore, we observed that trehalose could scavenge reactive oxygen species such as $O_2^{\cdot-}$ and H_2O_2 , which might play a more important role in conferring heat stress tolerance than protecting antioxidant enzymes, including superoxide dismutases (SOD), ascorbate catalases (CAT) and ascorbate peroxidases (APX) (data will be published). Therefore, trehalose may improve stress tolerance of plants by another role different from that as a compatible solute, and, as a multifunctional molecule, the exact role of trehalose under stress conditions should be paid more attention to. Treatment with trehalose improved rice saline tolerance but suppressed *Sal T* (a gene encoding a salt-induced lectin-like protein) induction by NaCl^[53]. In addition, genes encoding trehalose synthases (e. g. the *TPP* gene) were up-regulated more in salt-tolerant rice variety Nona (*Oryza sativa*, var. *Indica*), than in IR28 (*O. sativa*, var. *Indica*), the salt-sensitive one. But *Sal T* had lower expression in Nona^[58]. This may suggest that the lower *Sal T* expression in Nona might be a sign of tolerance to salt stress and trehalose might be a signal to mediate the lower *Sal T* expression in Nona. From above, it seems possible to improve stress tolerance of plants through regulating trehalose signal.

4 Concluding Remarks and Perspectives

As an excellent stress protectant, many studies have shown that increasing trehalose accumulation can improve the stress-resistance of plants by exogenous feeding or by genetic manipulation, and this foretells its bright perspectives in trehalose application. Evidence is accumulating that the metabolic pathway in plants has a role in sugar signaling. A detailed analysis of the interaction of metabolism with sugar signaling pathways will help us understand the metabolic basis of enhanced stress-tolerance. But lots of questions still remain unanswered. For example, as a sugar, the metabolic mechanism of improved stress-tolerance by trehalose has not been known distinctly. In addition, how trehalose is sensed, what signal transduction pathway it passes, how it correlates with plant hormones and how it affects resource allocation in plants are unknown. All of these questions await more experiments to be elucidated. In addition, more attention should be paid to basic researches about trehalose signaling and application of trehalose. The solution of these problems will help us not only much better understanding the role of trehalose but also avoiding pleiotropic effects caused by trehalose accumulation.

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