

Trehalose and Abiotic Stress in Biological Systems

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1. Introduction

Any non-living factors that affect negatively living organisms are reunited under the general term “abiotic stress” and its effects can be and are mitigated by a variety of defense mechanisms developed by the different biological systems in existence. Examples of abiotic stress are desiccation, salinity, high and low temperature. There are two general mechanisms used to counteract abiotic stress: avoidance and adaptation. In the case of avoidance, organisms migrate to deeper soil layers where temperatures are within tolerable range (Roelofs et al., 2008). Adaptation to stress is based on activation of stress defense gene pathways, which results in the production of heat shock proteins, LEA proteins, redox regulating proteins, different compatible solutes, cytochrome P450s (Roelofs et al., 2008).

Trehalose, also known as tremalose or mycose, a non-reducing disaccharide, is widely spread in biological systems: bacteria, yeast, fungi, lower and higher plants, as well as insects and invertebrates (Elbein, 2003), and its function is associated with tolerance against multiple abiotic stresses. It was discovered in 1832 by H.A. Wiggers in the ergot of rye and later isolated from mooshrooms by Mitscherlich in 1858, who called it mycose (Richards et al., 2002). In the same year Berthelot isolated a novel sugar from trehala-manna, a secretion left by different insects on leaves on Middle East. He named this new sugar “trehalique glucose” or trehalose (Richards et al., 2002). Initially trehalose was considered to be a rare sugar because it could only be extracted from trehala manna or the resurrection plant. Later Koch and Koch in 1925 discovered it in yeast and established basic protocols for trehalose isolation from yeast (Richards et al., 2002). Still, the cost of trehalose production was high enough so that it limited its use for commercial exploitation. In 1990's Hayashibara company in Japan discovered a method to mass-produce trehalose inexpensively from starch. The enzymes used in the process, maltooligosyl-trehalose synthase (MTSase) and maltooligosyl-trehalose trehalohydrolase (MTHase), are derived from a non-pathogenic soil bacteria, *Arthrobacter* sp. (Maruta et al., 1995).

Trehalose has multiple functions, and some of them are species specific. In microorganisms trehalose appears to act as an energy source, during certain stages of development such as spore germination (Elbein, 2003). In anhydrobiotic organisms, trehalose is known to accumulate to high concentrations to survive complete dehydration (Drennan et al., 1993), by preserving the membranes during drought period (Crowe et al., 1984). Trehalose acts as a structural component in mycobacteria, being incorporated into glycolipids (Elbein, 1974). In *Escherichia coli*, trehalose protects against cold stress, presumably by stabilizing cell

membranes and preventing protein denaturation, whereas in yeast it plays a role in osmotic (Hounsa et al., 1998), heat, and desiccation tolerance (Hottiger et al., 1987), and it may act as a free radical scavenger (Benaroudj, 2001). Insects use trehalose from blood as an energy source during flight (Elbein, 1974). Even though in most plants trehalose does not participate directly in the alleviation of abiotic stress, it may act as a signaling molecule. Microarray analyses revealed that both trehalose and trehalose-6-phosphate are affecting the levels of genes involved in abiotic stress (Schluepmann et al., 2004; Bae et al., 2005). Trehalose accumulated by brine shrimp embryos when entering dormancy may act as a stabilizer during dormancy and as an energy source for the embryos when the dormancy period ends (Clegg, 1965). Nematodes, when dehydrated slowly, convert as much as 20% of their dry weight to trehalose, helping them survive dehydration (Crowe et al., 1992).

2. Trehalose biosynthesis

There are five known pathways reported in living organisms for trehalose biosynthesis (Fig.1). Some organisms possess only one pathway, whereas others use multiple pathways, which are used depending on the stress affecting the organism (Paul et al., 2008).

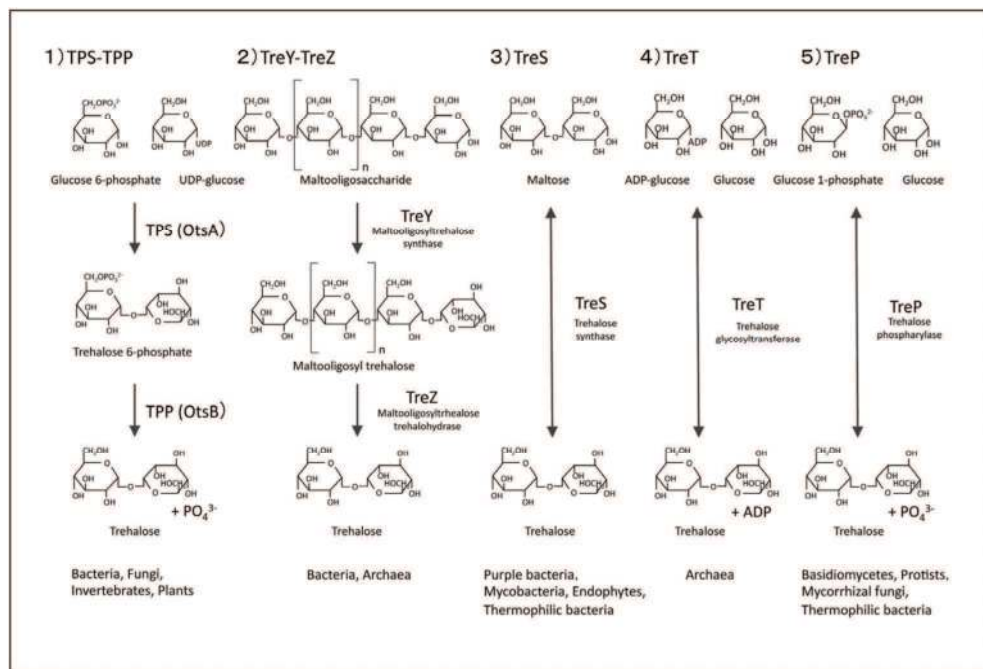


Fig. 1. Trehalose biosynthesis pathways in living organisms

2.1 TPS-TPP (OtsA-OtsB) pathway

TPS-TPP (OtsA-OtsB) pathway is a two steps process and it is the most common pathway for trehalose biosynthesis. It is present in both prokaryotes and eukaryotes (archaea, bacteria, fungi, plants and arthropods) (Paul et al, 2008). In plants, trehalose 6-phosphate

synthase (TPS) catalyzes the synthesis of the intermediate trehalose-6-phosphate from glucose-6-phosphate and Uridine Diphosphate (UDP)-glucose, and then trehalose-6-phosphate phosphatase (TPP) catalyzes the dephosphorylation of trehalose-6-phosphate to trehalose. In bacteria OtsA and OtsB enzymes catalyze the conversion of glucose-6-phosphate and UDP-glucose to trehalose, whereas in yeast TPS1 and TPS2 (homologues of TPS and TPP, respectively) are catalyzing the process. If in plants and bacteria the two trehalose biosynthesis enzymes are separate entities, in yeast the TPS1 (TPS homologue) and TPS2 (TPP homologue) are part of a complex that contains two other regulatory subunits, TPS3 and TSL1 (Bell et al., 1998).

2.2 TreY-TreZ pathway

Initially this pathway was discovered in *Arthrobacter* sp. (Maruta et al., 1995) and it is also a two-step pathway, in which maltodextrines are converted to trehalose. In the first step, maltooligosyltrehalose synthase (TreY) catalyzes the conversion of maltopentaose into maltooligosyl trehalose by intramolecular transglycosylation, and in the second step, maltooligosyltrehalose trehalohydrolase (TreZ) hydrolyzes the maltooligosyl trehalose, releasing free trehalose (Maruta et al., 1995). This pathway is also found in other bacterial species such as *Rhizobium* (Maruta et al., 1996a), *Bradyrhizobium japonicum* (Sugawara et al., 2010) and *Corynebacterium* (Tzvetkov et al., 2003), but is missing in other major bacterial groups including *E. coli* and *Bacillus subtilis*. Archaea *Sulfolobus* also uses this pathway for trehalose synthesis (Maruta et al., 1996b).

2.3 TreS pathway

The TreS pathway is a reversible transglycosylation reaction in which trehalose synthase (TreS) converts maltose, a disaccharide with α,α -1,4 linkage between the two glucose molecules, to trehalose. Trehalose synthase was first cloned from *Pimelobacter* sp. R48 (Nishimoto et al., 1995) and so far it has been detected only in bacteria (Paul et al., 2008). Due to the reversible nature of the enzyme, TreS contributes trehalose synthesis during osmotic stress in *Pseudomonas syringae* (Freeman et al., 2010), while TreS functions in trehalose catabolism in *B. japonicum* (Sugawara et al., 2010).

2.4 TreT pathway

TreT pathway involves the reversible formation of trehalose from ADP-glucose and glucose and it is catalyzed by trehalose glycosyltransferase (TreT) (Qu et al., 2004). TreT appears both in archaea and bacteria (Paul et al., 2008), and it was first reported in the hyperthermophilic archaea *Thermococcus litoralis* (Qu et al., 2004).

2.5 TreP pathway

TreP is the second trehalose synthesis pathway found in both prokaryotes and eukaryotes. It is a potential reversible reaction that converts glucose-1-phosphate (G1P) and glucose into trehalose, catalyzed by trehalose phosphorylase. The pathway was first discovered in *Euglena gracilis* (Belocopitow & Marechal, 1970) and later found in mushrooms and bacteria (Paul et al., 2008).

3. Trehalose roles in abiotic stresses

Trehalose involvement in tolerance to abiotic stress has been documented in numerous organisms, both prokaryotes and eukaryotes. The effects of desiccation, salt, high and low

temperature stresses have been shown to be averted by trehalose. The information is by no means complete and future studies may reveal trehalose implication in the fight against abiotic stresses in additional species.

3.1 Desiccation stress

Water is essential to the existence of life. Not only it is a basic component of living organisms, but also it is critical for their survival. However, there are organisms that can forgo water for extended periods of times, even for decades or centuries. Anhydrobiotic organisms can survive almost complete dehydration, the term anhydrobiosis literally meaning in Greek “life without water”. Such organisms are the invertebrates rotifers, tardigrades, brine shrimp and nematodes, but also certain resurrection plants, and microorganisms like baker's yeast (*Saccharomyces cerevisiae*) (Crowe et al., 1992).

Many of the anhydrobiotic organisms accumulate high concentrations of trehalose during drought stress. In the case of desiccation, water loss can be extremely high, as much as 99% (Strom et al., 1993). Among the protecting disaccharides that accumulate during drought, trehalose is the most effective in stabilizing dry membranes (Crowe et al., 1992). During dehydration, membranes are destabilized because of lipid phase transitions and vesicle fusion (Crowe & Crowe, 1990). Trehalose, even in small quantities, inhibits vesicles fusion completely and depresses the phase transition temperature of dry lipids, maintaining them in liquid crystalline phase in the absence of water (Crowe et al., 1992). It appears that during dehydration or freezing trehalose molecules replace bound water normally associated with biological structures (Donnamaria et al., 1994). Because of its high hydration potential, trehalose may stabilize dry biological membranes and proteins by hydrogen bonding of its hydroxyl groups to the polar groups of proteins and phosphate groups of membranes (Kawai et al., 1992).

Another mechanism by which trehalose protects against desiccation stress is vitrification. Trehalose has the tendency to form a protective glass-like structure that has a low reactivity, making it more stable than other disaccharides due to its non-reducing character. In this hygroscopic glass-like structure, trehalose is extremely stable both at high temperature and when completely desiccated and may hold biomolecules in a form that allows them to return to their native structure and function following rehydration (Crowe & Crowe, 2000). Trehalose glass is suggested to have such a great stability because a small addition of water may form trehalose dihydrate on the outer surface of the glass, which may result in a structure that encloses the inner glass, isolating it (Richards et al., 2002).

3.1.1 Bacteria

Trehalose involvement in bacteria resistance to desiccation stress has been studied extensively. *Nostoc commune* is a terrestrial cyanobacterium that can survive more than a hundred years in desiccated state (Lipman, 1941; Cameron, 1962). When exposed to drought, in addition to the production of large amounts of extracellular polysaccharides, which have an important role in desiccation tolerance, *N. commune* also accumulate trehalose (Sakamoto et al., 2009; Klahn & Hagemann, 2011). Other cyanobacteria that accumulate trehalose during drought stress are *Phormidium autumnale* and *Chroococidiopsis* sp. (Hershkovitz et al., 1991). Trehalose synthesis is activated in response to water loss due to desiccation process, whereas when the water becomes available and the cells rehydrate trehalose content in the cells decreases (Sakamoto et al., 2009). Other cyanobacteria, like

Anabena and *Nostoc flagelliforme*, accumulate trehalose but not in high enough quantities to be able to offer protection as a molecular chaperone. In these cases, trehalose may act indirectly in alleviating drought stress, by regulating the expressions of molecular chaperone-related genes (Higo et al., 2006; Wu et al., 2010).

Rhizobia, soil bacteria that live in symbiosis with legumes are important to agriculture because of their biological nitrogen fixation capacity. *Bradyrhizobium japonicum*, the root nodule symbiont of soybeans, accumulates trehalose using three independent trehalose biosynthesis pathways (Streeter, 2006). Interestingly, mutants of the cells lacking the TreS degradation pathway showed a low survival under desiccation stress (Sugawara et al., 2010). This happened presumably because the high concentrations of trehalose affected the refolding and reactivation of denatured proteins by molecular chaperones and explains the reason why trehalose is quickly degraded after stress has ceased (Singer & Lindquist, 1998). Trehalose accumulation in bacteria influences as well the symbiont plants drought resistance. Rhizobacteria engineered to overexpress trehalose biosynthetic genes improved the drought tolerance of the plants inoculated with the modified rhizobia strains. Common bean plants (*Phaseolus vulgaris*) inoculated with *Rhizobium etli* overexpressing trehalose-6-phosphate synthase recovered completely when exposed to drought stress as opposed to plants inoculated with the wild type strain, which wilted and died (Suarez et al., 2008). Maize plants inoculated with *Azospirillum brasilense* overexpressing trehalose biosynthetic genes had an 85% of survival following drought stress compared to 55% survival rate in the case of the plants inoculated with the untransformed strain (Rodriguez-Salazar et al., 2009).

3.1.2 Fungi

Trehalose is widely distributed in fungi and it accumulates in both vegetative and reproductive stages, and at particularly high concentrations in periods with reduced growth rates and during starvation (Thevelein, 1984). Trehalose is also present in the extra-radical mycelium as well as in spores of arbuscular mycorrhizal fungi (BeCARD et al., 1991).

Log-phase cultures of yeast have low concentrations of trehalose and are quite susceptible to dehydration, but as they enter the stationary phase of growth the levels of trehalose increase (Elbein, 2003). A study of desiccation tolerance of yeast cells subjected to temperature shifts revealed a clear correlation between the cells trehalose content and the changes in desiccation tolerance, demonstrating the trehalose function as a protectant against desiccation (Hottiger et al., 1987).

3.1.3 Plants

The presence of trehalose in higher plants was discovered relative recently, and most of the reports were referring to a few desiccation tolerant plants (Bianchi et al., 1993; Drennan et al., 1993; Albini et al., 1994). Following whole genome sequencing, *Arabidopsis* genome has been found to contain eleven putative TPS and ten putative TPP genes, whereas in the rice genome nine TPSs and nine TPPs have been identified. Transgenic *Arabidopsis* plants overexpressing *AtTPS1* (Avonce et al., 2004) exhibited drought stress tolerance as well as glucose and ABA insensitive phenotypes. The altered regulation of genes involved in ABA and glucose signaling during seedling vegetative growth may account for the insensitivity, pointing out *AtTPS1* and/or trehalose-6-phosphate as a major player in gene regulation and signaling during seedling development. *Arabidopsis csp-1* mutant, with a point mutation in the synthase domain of another *Arabidopsis* TPS, *AtTPS6*, is also drought-tolerant (Chary et al., 2008).

Typically, trehalose does not accumulate in plants in quantities high enough to directly protect against abiotic stress as a compatible solute, the way it accumulates in other organisms. Transgenic plants engineered to overexpress microbial trehalose biosynthesis genes accumulated low levels of trehalose and still became tolerant to abiotic stresses, specifically to drought stress. Tobacco and tomato plants transformed with yeast *TPS1* gene under the control of 35S promoter proved to be drought tolerant (Romero et al., 1997; Cortina & Culianez-Macia, 2005). The drawbacks of the studies were the growth aberrations of the transgenic plants – they presented stunted growth (tobacco) and abnormal root development (tomato). The growth abnormalities present in the engineered plants are most probably due to the accumulation of trehalose-6-phosphate, who proved to be an essential player in plant development, since homozygous *tps1* mutants are embryo-lethal (Eastmond et al., 2002). In addition, trehalose-6-phosphate has been found to act as an inhibitor of SnRK1, a hexokinase that is an important transcriptional regulator of metabolism, growth and development in plants (Zhang et al., 2009; Paul et al., 2010). Drought tolerant tobacco plants which did not present any growth abnormalities were obtained by targeting the *TPS1* gene expression to chloroplast or by using bifunctional fusion yeast trehalose synthesis genes (Karim et al., 2007).

3.1.4 Tardigrades

Tardigrades are microscopic animals, also known as water bears, which show an extraordinary tolerance to variety of extreme environmental conditions, particularly anhydrobiosis (Welnicz et al., 2011). In some species, the trehalose levels are increased during the induction of anhydrobiosis, but in others there was no difference in trehalose levels between the desiccated and hydrated specimens. In addition, the absolute levels of trehalose detected in tardigrades are much lower than those detected in other anhydrobiotic organisms, indicating that trehalose may have a specific function connected to desiccation, but the nature of that function is not currently known (Welnicz et al., 2011).

3.1.5 Insects

Polypedilum vanderplanki lives in temporary rock pools in tropical Africa. When the pool dries up, the larvae become dehydrated and remain desiccated until the next rain (Fig. 2). *P. vanderplanki* is the largest multicellular organism known to be able to withstand almost complete dehydration for up to 17 years. Cryptobiotic larvae can withstand extreme temperatures from -170°C to + 106°C and recover completely within an hour when supplied with water (Watanabe et al., 2003). Desiccation stress induces trehalose synthesis in larvae as well as the *TreT1* gene expression. *TreT1* is a trehalose specific transporter, which during the desiccation stress transports the trehalose synthesized in the fat body to the hemolymph (Kikawada et al., 2007).

3.2 Salt stress

Salt stress affects organisms in two major ways. Low water potential causes loss of water and turgor pressure, whereas the high ionic strength of the surrounding environment creates a continuous flux of inorganic ions into the living cells. Living organisms maintain their turgor pressure and cell volumes within acceptable limits by accumulating organic osmolytes, called compatible solutes (sugars, polyols, free aminoacids and their derivatives, quaternary amines and their sulfonium analogues, sulfate esters and small peptides (Kempf

et al., 1998). Compatible solutes participate in alleviating salt stress in two major ways. First, they lower the osmotic potential of the cytoplasm, maintaining the normal turgor pressure of the cells (Kempf et al., 1998). Second, they serve as stabilizers of proteins and cell components against the denaturing effects of high ionic strength (Hinch & Hagemann, 2004). Among the compatible solutes, trehalose occupies an important place, acting as a stress protectant in both prokaryotes and eukaryotes.

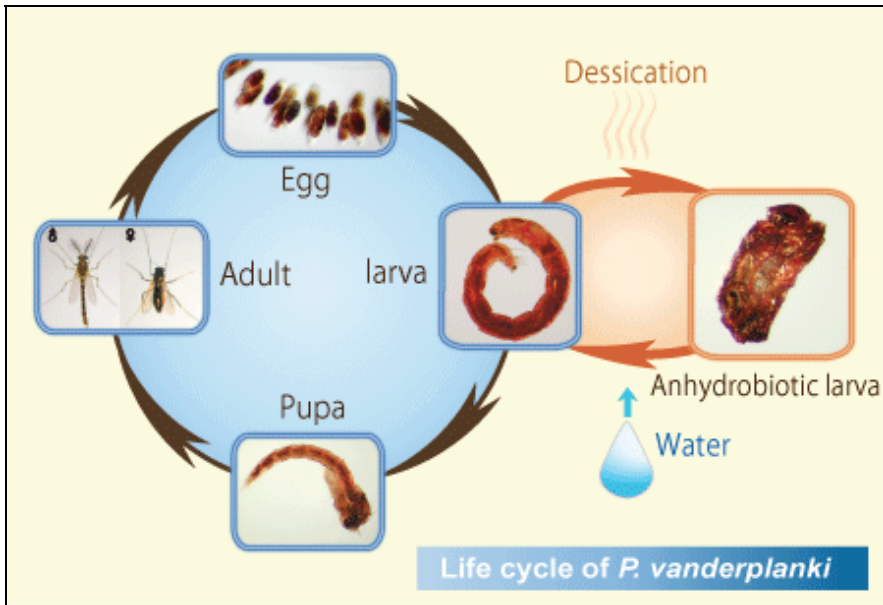


Fig. 2. Life cycle of *Polypedilum vanderplanki*. The larva stage animal shows complete desiccation tolerance (Reproduced with permission from Anhydrobiosis Research Group, National Institute of Agrobiological Sciences, 2009).

3.2.1 Bacteria

E. coli cells adapt to osmotic stress by accumulating in the cytoplasm trehalose produced endogenously. Excess trehalose is excreted and then degraded by periplasmic trehalase (treA) to glucose, which is subsequently reutilized by the cells (Strom et al., 1993). Furthermore, *E. coli*, *S. meliloti*, *B. japonicum* mutants lacking trehalose biosynthesis genes are sensitive to osmotic stress. (Strom et al., 1993; Dominguez-Ferreras et al., 2009; Sugawara et al., 2010).

Most of cyanobacteria are living in waters of different or changing salinities. Those who dwell in fresh water habitats are adapted to a low osmotic strength environment. Nevertheless, most freshwater cyanobacteria are able to withstand at least partially increasing salt concentrations. Among the compatible solutes that are mostly induced to accumulate in response to low osmotic stress are trehalose and sucrose (Klahn et al., 2011). Trehalose accumulation in cyanobacteria was first demonstrated in *Rivularia atra*, which live in the tidal zone of the coastal waters (Reed & Stewart, 1983). Since then it was revealed that more than forty strains accumulate trehalose when grown on media enriched with NaCl, and in twenty of them trehalose is the major compatible solute accumulated (Hagemann,

2011). The mechanism by which trehalose helps alleviate the stress condition is not salt-specific, but is rather related to the ability of trehalose to stabilize membranes and protein structure. Compatible solutes transport is wide spread in bacteria and many of them (in particular heterotrophic bacteria) prefer to import the stress protectants instead of synthesizing them. However, cyanobacteria use compatible solutes synthesized de novo and use the transporters to uptake their compatible solutes that have diffused into the periplasm (Hagemann, 2011). A transporter with uptake specificity for sucrose, trehalose and glucosylglycerol has been discovered for the first time in *Synechocystis* (Mikkat et al., 1996). The soil bacterium *Corynebacterium glutamicum* utilizes trehalose as a compatible solute depending on the environmental conditions. When nitrogen is present in sufficient quantities, trehalose plays only a marginal role in osmoprotection and proline is the dominant compatible solute, whereas when nitrogen is scarce, trehalose becomes dominant. In addition, trehalose accumulation increases if maltose is used instead of sucrose as carbon source (Wolf et al., 2003).

Salinity stress affects negatively the symbiotic interactions between rhizobia and legume plants, limiting nitrogen fixation and reducing crop yields. Trehalose accumulates in rhizobium *Bradyrhizobium japonicum* in response to salt treatment. Mutant strains lacking the trehalose biosynthetic genes failed to grow on salt containing medium, indicating that trehalose plays a role as a osmoprotectant for growth under salt-induced osmotic stress (Sugawara et al., 2010). In a different study investigating four rhizobial strains isolated from nodules of *Phaseolus vulgaris* under salt-stress conditions revealed that all strains under study accumulated trehalose (Fernandez-Aunión et al., 2010).

3.2.2 Fungi

Arbuscular mycorrhizal fungi colonize plant root systems of over 80% of terrestrial plant species and have been shown to promote plant growth and salinity tolerance by numerous studies (Evelin et al., 2009). *Glomus intraradices* exposed to osmotic stress did not present major changes in trehalose metabolism. Only moderate transient activations of trehalose-6-phosphate phosphatase and neutral trehalase were observed (Ocon et al., 2007).

3.2.3 Plants

Rice *OsTTP1* and *OsTTP2* are transiently induced by cold, salt and drought stress as well as external ABA applications (Pramanik & Imai, 2005; Shima et al., 2007). Garcia et al. (1997) reported as well trehalose accumulation in small amounts in rice roots 3 days following salt stress. External applications of low concentrations (up to 5 mM) of trehalose reduced Na⁺ accumulation and growth inhibition and higher concentrations (10 mM) prevented chlorophyll loss in leaf blades and preserved root integrity (Garcia et al., 1997). Alfalfa (*Medicago sativa* L.) plants exposed to salt stress accumulated trehalose in roots and bacteroids, but the quantities detected were too low to account for an osmoprotectant role for trehalose (Fougere et al., 1991). In *Medicago truncatula* trehalase activity in nodules was downregulated under salt stress, permitting trehalose accumulation, but again in low quantities to efficiently contribute to osmoprotection (Lopez et al., 2008).

Tomatoes engineered to overexpress yeast trehalose synthesis genes are resistant not only to drought, but also to salt and oxidative stresses (Cortina & Culiñez-Macia, 2005). Rice plants overexpressing bacterial fused trehalose synthesis genes under the control of tissue-specific or stress-dependent promoters accumulate trehalose and are salt, drought, and low temperature stress tolerant, without showing growth abnormalities (Garg et al., 2002).

3.3 Low and high temperature stress

Biological membranes are affected during low temperature stress, as their fluidity decreases. Protein denaturation and aggregation happen both under low and high temperature stresses. As a compatible solute trehalose, can prevent protein degradation and aggregation. It can also stabilize biological membranes, by hydrogen bonding with the phosphate groups.

3.3.1 Bacteria

Kandror et al. (2002) reported a protective role of trehalose in cold adaptation of *E. coli*. Strains deficient in trehalose biosynthesis are much more sensitive to cold stress than wild type. However, the deficient strains complemented with trehalose biosynthesis genes have their cold resistance restored. The authors suggest that the mechanisms of trehalose protection against cold include protection of protein integrity, free radical scavenger activity *in vivo* defending against oxidative damage, and cell membranes stabilization. Some of the bacteria that live in high temperature saline environments, such as *Thermus thermophilus*, and hyperthermophilic archaea, like *Pyrobaculum aerophilum*, accumulate primarily trehalose as a compatible solute (Santos & da Costa, 2002).

3.3.2 Fungi

The most studied abiotic stress that induces trehalose in fungi is heat stress. The high level of trehalose in fungal spores increases their resistance to heat stress. Trehalose biosynthesis genes as well as trehalase, responsible for trehalose breakdown are up regulated, resulting in trehalose accumulation. In the yeast *S. cerevisiae* trehalose induced by heat shock not only stabilizes protein structure, but also suppresses aggregation of the proteins that have already been denatured. However, following heat stress, trehalose is degraded rapidly allowing the molecular chaperones to renature the proteins by refolding (Hottiger et al., 1987). Damage done to protein structure and cell membranes during heat stress is due at least partly to reactive oxygen species (ROS) (Davidson et al., 1996). Exposing yeast cells to increased temperatures, trehalose also increased markedly their resistance to oxidative stress (Benaroudj et al., 2001).

Trehalose appears to also have a role in low temperature stress. Hino et al. (1990) reported a correlation between trehalose intracellular accumulation and freeze tolerance of *S. cerevisiae*. When trehalose was accumulating constitutively in the yeast *S. cerevisiae* overexpressing *TPS1* and *TPS2* genes, and *Schizosaccharomyces pombe* overexpressing *TPS1* gene, the strains became resistant to multiple abiotic stresses, including freezing stress (Soto et al., 1999; Mahmud et al., 2010). Following cold stress, when the yeast is returned to non-stress temperature, trehalose and trehalose synthesizing enzymes levels are dropping rapidly (Kandror et al., 2004). *Hebeloma* spp., an ectomycorrhizal basidiomycetes, who can survive sub-zero temperatures, synthesize trehalose, arabitol and mannitol when exposed to freezing stress (Tibbett et al., 2002).

3.3.3 Plants

Rice *OsTPP1* and *OsTPP2* are transiently induced by cold, salt and drought stress as well as external ABA applications (Pramanik & Imai, 2005; Shima et al., 2007). Trehalose was also transiently induced following chilling stress, and its accumulation coincided with the phase change of glucose and fructose levels (Pramanik and Imai 2005). In *Arabidopsis*, *AtTPS5* has a role in thermotolerance. *AtTPS5* interacts with MBF1c, a transcriptional activator that is a key regulator of thermotolerance (Suzuki et al., 2008).

Arabidopsis plants engineered with yeast *TPS1* gene under the control of either 35S promoter or a yeast *TPS1-TPS2* fused-genes construct under the control of a stress regulated promoter, accumulated trehalose at low levels and are resistant to abiotic stresses, including freezing and heat stress. If the plants transformed with the first construct displayed aberrant growth, color and shapes, plants transformed with the second construct did not show any morphological or growth abnormalities (Miranda et al., 2007).

3.3.4 Nematodes

In nematodes, trehalose induces thermotolerance by preventing damage under heat stress. In addition, trehalose extends the nematodes life-span, possibly by protecting against heat-stress associated damage (Honda et al., 2010). Arctic nematode *Panagrolaimus davidi* accumulates an increasing amount of trehalose following cold temperature acclimation, which may help in membrane stabilization and protect against freeze-induced dehydration (Wharton et al., 2000).

3.3.5 Insects

Exposure to a mild cold stress over a period of few minutes to a few hours can increase the cold tolerance of some insects. *Drosophila melanogaster* and *Sarcophaga crassipalpis* flies show an increase of their trehalose levels following cold treatment, increase correlated with an improved chill tolerance (Clark & Worland, 2008). Also, the prepupal larvae of the sawfly *Trichiocampus populi*, who can survive at -30°C for several hours, contain high concentrations of trehalose (Ohtake & Wang, 2011).

4. Trehalose uses in relation to abiotic stress

Due to the fact that trehalose proved to be a protectant compound under abiotic stress conditions, it has been and may be used in countless applications in pharmaceutical industry, agriculture, food industry, cosmetics industry, medicine, and research.

4.1 Agriculture and food industry

Since trehalose has been found to participate in increasing tolerance to abiotic stresses in other organisms, many attempts have been made to engineer plants with microbial trehalose biosynthetic genes from OtsA-OtsB pathway in order to create stress tolerant plants: tobacco (Holmstrom et al., 1996; Goddijn et al., 1997; Romero et al., 1997; Pilon-Smits et al., 1998; Lee et al., 2003; Han et al., 2005; Karim et al., 2007), rice (Garg et al., 2002; Jang et al., 2003), tomato (Cortina & Culianez-Macia, 2005), potato (Goddijn et al., 1997) and *Arabidopsis* (Karim et al., 2007; Miranda et al., 2007). The first trials were partially successful, trehalose accumulated, albeit at a low level, the plants were stress tolerant, however they displayed abnormal phenotype characteristics (Goddijn et al., 1997; Romero et al., 1997; Pilon-Smits et al., 1998; Cortina & Culianez-Macia, 2005). Nonetheless, subsequent studies solved the phenotype problem by using fused bacterial trehalose biosynthesis genes, directing the gene constructs to chloroplasts (Garg et al., 2002; Jang et al., 2003; Karim et al., 2007; Miranda et al., 2007), or engineering the plants with alternate trehalose biosynthesis genes, as trehalose phosphorylase (TreP), which circumvented the production of trehalose-6-phosphate (Han et al., 2005).

The symbiotic relationship between rhizobia and legumes has a considerable impact not only on the legumes yields but also on the significant amount of the fixed nitrogen that

remains in the soil for future crops use. A way to encourage the formation of the legume-rhizobia symbiosis could be the application of rhizobia to legume seeds prior to planting in the field. However, the percent of survival of rhizobia applied in this manner is very low, less than 5%, because of rapid desiccation (Roughley et al., 1993). By supplying external trehalose (3 mmol l⁻¹) to *Bradyrhizobium japonicum* strain USDA 110, the concentration of trehalose in the cells increased threefold and bacteria survival in response to desiccation increased by two to fourfold (Streeter, 2003).

Trehalose role in protecting agricultural products may not be resumed only in helping the direct preservation. For instance, the yeast *Pichia anomala* has antifungal activities and could be used in biocontrol activities against fungal contaminants on fruits and grains. Large quantities of yeast have to be produced and processed for commercial use. The end product should have a long-shelf life, preferably should be able to withstand high temperatures, in the same time keeping to a minimum the production cost in order to be viable from an economical point of view. Trehalose is used in liquid formulations as well as in freeze-drying and vacuum-drying techniques (Melin et al., 2011).

The ability of trehalose to protect protein structure suggested its use in food packaging and preservation. Fresh fruits, herbs, and vegetables are preserving their color, taste and flavors when dried after a brief immersion in trehalose solution (Iturriaga et al., 2009). Superoxide dismutase (SOD) in plants acts as an antioxidant and protects cell components against oxidative damage by reactive oxygen species (Alscher et al., 2002). SOD-like activity of vegetables (carrots, cucumber, spinach onion) was preserved upon drying fresh vegetables with trehalose (Ohtake & Wang, 2011). Trehalose in its glass form encases and protects biomolecules, permitting them to return to their native structure and function upon rehydration (Crowe & Crowe, 2000). Fresh banana, strawberry, mango, avocado, apple, and raspberry, pureed in the presence of trehalose and dried at 25–50°C, kept their color and aroma during prolonged storage. Volatile aromatics are trapped within the trehalose nonpermeable glass and released only after reconstitution of the product (Ohtake & Wang, 2011).

Because of its shielding properties, trehalose has been included as a food additive in Japanese rice cake for protection against low temperature and freezing stresses (Ohtake & Wang, 2011). Freeze-tolerant yeast strains, accumulate trehalose when exposed to freezing (Hino et al., 1990). These strains retain their fermentative ability and bread leavening activity up to six weeks of frozen storage, maintaining their ability to produce good quality bread following freezing (Hino et al., 1987). As trehalose had been found to be able to suppress fatty acid degradation from heat and also from free radical oxidation (Higashiyama, 2002), it is effective in suppressing the formation of unpleasant odors associated with cooking fish (Ohtake & Wang, 2011).

4.2 Cosmetics industry

Trehalose has been found to suppress the unpleasant odors emitted by human skin by up to 70%, which makes it a very good candidate for use in facial and body creams and body deodorants (Higashiyama, 2002). In addition, trehalose incorporated in cosmetic products may enhance their shelf life and mask the odor of active ingredients and their degradation products, due to its antioxidation properties (Ohtake & Wang, 2011).

The high water retention capabilities of trehalose make it useful as a moisturizer in cosmetics (Hyde et al., 2010)

4.3 Medicine and pharmacy

As trehalose proved to be able to suppress peptide aggregation (Singer & Lindquist, 1998), it has been used to reduce the symptoms of Huntington's disease. In the cells of patients suffering of this disease, the mutant protein huntingtin forms insoluble aggregates that are thought to produce the disease. Oral administration of trehalose inhibited the formation of huntingtin aggregates and improved the associated motor dysfunction in a transgenic mouse model of Huntington disease (Tanaka et al., 2004).

Researchers at Tokyo University developed an organ preservation solution, extracellular-type trehalose-containing Kyoto (ET-Kyoto) solution, that was successfully used in clinical lung transplantation (Ohtake & Wang, 2011).

Another application for trehalose use is the formulations of heat stable vaccines. An optimized *Salmonella enterica* serovar Typhi oral typhoid vaccine formulated with trehalose, methionine and gelatin proved to be stable for more than four weeks at 37°C. This represents a clear advantage for developing countries as it allows for longer shelf life and the vaccine distribution without the need of refrigeration (Ohtake et al., 2011).

4.4 Research

Unstable molecules such as antibodies can be dehydrated at room temperature or 37°C in the presence of trehalose, maintaining their activity after months in storage (Iturriaga et al., 2009). Dried proteins adopt the same configuration as they do in hydrated state when they are stabilized with trehalose, because trehalose prevents degradation by deamidation, oxidation, and aggregation (Ohtake & Wang, 2011).

In plant research, *Arabidopsis* AtTPS1 gene can be employed as a selectable marker gene during the process of plant transformation, using glucose as a selective agent (Iturriaga et al., 2009). The AtTPS1 gene of *A. thaliana* encodes the TPS1 enzyme, which confers glucose insensitivity to seeds and tissues of plants overexpressing this gene when cultivated under tissue-culture conditions (Avonce et al., 2004).

5. References

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Abiotic Stress in Plants - Mechanisms and Adaptations

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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly divided into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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