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Effect of trehalose on growth and stress tolerance in crops by using bioinoculants

El efecto de la trehalosa en el crecimiento y tolerancia al estrés de los cultivos mediante el uso de bioinoculantes

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ABSTRACT

Trehalose biosynthetic is an important pathway that linked to abiotic stress tolerance. Recent research findings showed that the trehalose metabolic pathway is important for the growth and development of the plant. In plants, trehalose production seemed to be exclusively reserved for stress resistant plants which living in extreme habitats. In variety of plant species to improve the stress tolerance and yield particularly under stress condition, several attempts to engineer plants that produce more trehalose. In many studies have observed the regulatory role of trehalose-6-phosphate, a precursor of trehalose, play an important role in sugar metabolism, growth and development in plants. Trehalose-6-phosphate influences the starch and sucrose accumulation in leaves during day time regulates starch degradation at night to demand for sucrose. It is necessary to understand about the potential role of trehalose as a metabolite in abiotic stress responses and interactions of plants with bacterial and fungal pathogens, rhizobia, mycorrhizae and non symbiotic rhizobacteria.

Key words - Abiotic and biotic stress, Heavy Metals, Rhizobacteria, Trehalose

RESUMEN

La trehalosa biosintética es una ruta importante que está relacionada con la tolerancia al estrés abiótico. Investigaciones recientes demostraron que la ruta metabólica de la trehalosa es importante para el crecimiento y desarrollo de una planta. Para las plantas, la producción de trehalosa parecía estar reservada exclusivamente para las plantas resistentes al estrés, las cuales viven en hábitats extremos. Con el fin de mejorar la tolerancia al estrés de una variedad de especies vegetales y el rendimiento de ellas, especialmente en condiciones de estrés, se han realizado varios intentos para diseñar plantas que produzcan más trehalosa. En muchos estudios se ha observado la función reguladora de la trehalosa 6-fosfato, la cuál es precursora de la trehalosa y que juega un rol fundamental en el metabolismo de los azúcares, el crecimiento y desarrollo de las plantas. La trehalosa 6-fosfato influye en la acumulación del almidón y la sacarosa en las hojas en el día, y en la noche regula la degradación del almidón para luego exigir sacarosa. Es necesario entender el rol potencial de la trehalosa como un metabolito con respecto a las respuestas al estrés abiótico y las interacciones de las plantas con patógenos bacterianos y fungales, rizobios, micorrizas y rizobacterias no simbióticas.

Palabras clave: estrés abiótico y biótico, metales pesados, rizobacterias, trehalosa

INTRODUCTION

Trehalose is an non reducing sugar in which two glucose units are linked in alpha, alpha-1, 1-glycosidic linkage (alpha-D-glucopyranosyl-1,1-alpha-D-glucopyranoside) occurs in a large variety of organisms, ranging from bacteria to invertebrate animals, where it serves as an energy source or stress and osmoprotectant (Satoshi ohtake *et al*., 2010). Trehalose is a source of energy and carbon, isolated from *Trehala* in the 19th century by French chemist Marcellin Berthelot (Jacques Luyckx *et al*., 2011). Many trehalose biosynthetic pathways have been identified in bacteria and archaea and also in eukaryotes. It may control certain metabolic pathways or even affect the growth of plants. Trehalose can protect proteins and cellular membranes from inactivation and denaturation caused by a variety of stress conditions like desiccation, dehydration, heat, cold and oxidation. Trehalose is present in an integral component of various glycolipids (John Edward Lunn *et al*., 2014**)**. It is present in different bacteria, including *Streptomyces hygroscopicus*, *Mycobacteria, Corynebacteria, E.coli* and *Rhizobium S*p, uses trehalose as an osmolyte and stress protectant (Rohit Ruhal *et al*., 2013). But in many organisms the function of trehalose is still not clear. In the animal kingdom trehalose was identified in insects particularly in the main blood sugar. In fungi trehalose originates from nodules during nodule senescence and as an excretion product. By using trehalose, plants produce higher homologs of sucrose such as raffinose and stachyose and these higher sucrose oligosaccharides will play a important role in stabilizing or protecting cells against stress(John Edward Lunn *et al*., 2014). The review is focus on tolerance mechanisms and more specifically the role of trehalose and its metabolism as putative compatible solute and its role in stress tolerance.

DIFFERENT TYPES OF STRESS FOR THE GROWTH OF PLANT

The external conditions adversely affect the growth, development and productivity of plants is referred as stress. Stresses trigger plant responses such as growth rates, alteration in gene expression, crop yield, cellular metabolism etc. A sudden changes in the environmental condition reflects the plant stress which leads to acclimation to the specific stress in a time dependent manner. Abiotic stress and biotic stress are the two primary categories of plant stress. Abiotic stress imposed on plants either by physical or chemical factors whereas biotic stress is by biological unit like insect, diseases etc. Plants exhibit several metabolic dysfunctions by some stresses to the plant by injury. If the stress is short term or mild the plant may recovered from the injuries while in severe stresses leads to death of the plant by inducing senescence and prevent seed and flowering formation (Gray & Brady 2016). The stress can be grouped into three categories as single, multiple individual and combined stresses. Only one stress factor which affect the plant growth and development is single stress whereas two or more stresses occurring at different time periods without any overlap is multiple individual. In summer the co-occurrence of heat and drought is combined abiotic stress whereas both fungal and bacterial pathogen attacking a crop at the same time is the combined biotic stress (Prachi Pandey *et al*., 2017).

PHYSIOLOGICAL BASICS OF ABIOTIC STRESS TOLERANCE IN PLANT

Drought stress affects the plant hormone by balance to reduce the endogenous cytokinin level and increasing the levels of abscisic acid (ABA) in the leaves, thereby eliciting stomatal closure. The cytokinin–ABA antagonism might be the result of metabolic interactions, since they share common biosynthetic origin (Figueiredo *et al.,* 2008). Because nutrients are carried to the roots by water, soil moisture deficit therefore decreases nutrient diffusion over short distances and the mass flow of water-soluble nutrients such as nitrate, sulfate, Ca, Mg, and Si over longer distances (Barber, 1995). Drought reduces the availability of CO_2 for photosynthesis, which can lead to the formation of reactive oxygen species (ROS) such as superoxide radicals. Active oxygen species can act on unsaturated fatty acids and loosen the membranes, and finally affect the DNA. Drought increases the vulnerability to nutrient losses from the rooting zone through erosion (Rajib Karmakar *et al*., 2016). Under drought situations, roots are known to extend their length, increase their surface area, and alter their architecture in an effort to capture less mobile nutrients such as phosphorus (Lynch and Brown 2001). Drought also disrupts root–microbe associations that play a major role in plant nutrient acquisition. Figure - 1 shows the biotic and abiotic stress in plants.

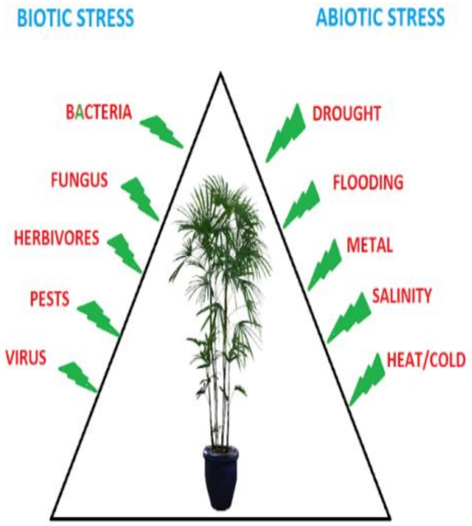

Figure - 1 Biotic and Abiotic stresses in plants

DROUGHT STRESS MICROBIAL ECOLOGY

The roots recruit microbiomes from the soil and the drought - treated root microbiome is dependent on the response of soil bacterial communities. The microbial diversity in the soil is significantly impacted by soil. The shift in the soil microbiome under drought condition involve the relative abundance changes rather than abolition of drought - susceptible taxa and concomitant tolerants that helps to find out the lack of change in alpha - diversity. Under drought condition, an increase in the ratio of gram - positive to gram - negative bacteria are observed (Fuchslueger *et al*., 2016). In moisture - limited soils the relative abundance shift decreases gram negative phyla such as *Proteobacteria*, *Verrucomicrobia* and *Bacteroidetes* (Yuste et al., 2014) and increases in gram positive phyla such as *Firmicutes* and *Actinobacteria* (Hartmann *et al*., 2017). The distinct drought susceptibilities between gram positive and gram negative bacteria shows difference in substrate preference and their metabolic capacities. Oligotrophic microorganisms are characteristically droughted environments that is, they are nutrient poor but oxygen rich. Microorganisms under this condition are oligotrophs are known for being slow growers but sustain under poor conditions (Kurm *et al*., 2017). In increased litter fall after rewetting copiotrophs are thrive under nutrient and water rich conditions (Hartmann *et al*., 2017). The oligotrophic bacteria in droughted soils involved in the degradation of complex plant polysaccarides and decreased abundance in targeting oligisaccharides (Martiny *et al*., 2016). The oligotrophic-copiotrophic distinction overlaps with gram positive and gram negative bacteria. Gram positive bacteria are more metabolically hardy compare to gram negative bacteria because they can utilize inorganic nitrogen to produce extracellular enzymes that degrade complex organic compounds that are relatively abundant in droughted soils (Treseder *et al*., 2011).

Labile organic carbon is increasingly scare within soil under drought condition (Thaysen *et al*., 2017) and the rate of plant derived carbon transfer go down to the microbes (Ruehr *et al*., 2009). So that microbial communities switch to degrading more recalcitrant carbon sources within plant organic matter (Bradford *et al*., 2008). Under drought condition, as part of osmotic adjustment the plant close the protein channels to prevent sugar transport to the rhizosphere. Indirect causes mediated by changes in the soil physicochemical properties are also known to play a important role in shaping microbial communities. For instance, low soil moisture reduces soil pore connectivity, raises solute concentrations in the remaining water, and limits substrate diffusion (Liptzin *et al*., 2011). The soils with limited water may decrease the overall ion content including sodium, potassium, calcium carbonate and redox sensitive compounds (Bouskill *et al*., 2016b). These changes in soil chemistry will exert an influence on the microbiome – in experiments analyzing the influence of various factors on soil bacteria, chemical properties including pH and ion content were significant in determining community composition and often on a taxa-specific basis (Gunnigle *et al*., 2017).

ROLE OF PLANT GROWTH PROMOTING RHIZOBACTERIA IN DROUGHT STRESS

Plant accomplishment of a drought-specific microbiome could be an evolved trait, where generations of repeated drought events have led to evolution of stable and beneficial plant-microbe interactions which improves the reproductive fitness of both plant and microbe. A drought-tolerant community achieved through soil attenuation, in which bacterial communities in soils exposed to drought have developed resistance, and thus the plant will have no choice but to recruit a beneficial microbiome. Under drought condition in sympatric soil, that is plant repeatedly grown in same soil can improve the crop performance such as biomass and drought responsive gene expression (Zolla *et al*., 2013). Even the crop not under stress will recruit the beneficial bacteria in the soil and enhance drought tolerance for other members of species. The relative health and fitness of the plant shall increases by accomplishment of microbes with plant growth promoting activities. A stable interaction between the plants and desired microbiome is an enchanting target for crop improvement through stress tolerance (Quiza *et al*., 2015). In a variety of plant species screening of putative plant growth-promoting bacteria (PGPB) *in vivo* on droughted plants is a frequent strategy used to confirm growth promotion (Cherif *et al.*, 2015). The drought tolerance in plant shall enhanced by PGPB are originally isolated and in some cases and in some cases enhance plant growth only under drought conditions (Rolli *et al*., 2015). By producing consortia of bacteria may have greater and synergistic effects at alleviating drought compare to individual genera (Timm *et al*., 2016). A consortium of 10 endophytic strains applied to hybrid poplar enhanced plant survival under water limitation through multiple distinct drought-response pathways (Khan *et al*., 2016).

A variety of PGP abilities are implicated in conferring drought tolerance, of which perhaps the most studied is the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACCd). Through ACCd activity, the plant hormone ethylene remains below inhibitory levels, maintaining normal root growth and delaying senescence under drought (Glick, 2004). PGPB are also known for synthesizing other phytohormones, including the auxin analog indole-3-acetic acid (IAA), which can enhance shoot and root growth among other plant developmental processes (Glick, 1995). During drought, PGPB involved in the nutrient cycling, diazotrophy, phosphorus solubilization, and siderophore synthesis (Kim *et al.*, 2012). They also been shown to enhance photosynthesis, increase fine root production and greater overall root surface area, and decrease stress volatile emission, which play an important role in the improvement of plant performance (Gagne-Bourque *et al*., 2016). Figure - 2 shows the plant growth *Rhizobacteria* in drought stress.

BIOSYNTHESIS OF TREHALOSE

Trehalose is a non-reducing disaccharide consisting of two units of glucose (α-D-glucopyranosyl-1,1-α-D-glucopyranoside) is widely spread in a variety of organisms such as bacteria, yeast, fungi, lower and higher plants, as well as insects and other invertebrates (Elbein *et al*., 2003). Figure - 3 shows the biosynthesis of trehalose. In abiotic stress tolerance an important pathway has been linked is trehalose biosynthetic pathway which is important for normal plant growth and development. In trehalose metabolic pathway, an intermediate product trehalose - 6 phosphate (T6P) is act as a sensor for available sucrose that influence the type response by changing environmental conditions. Trehalose - 6 phosphate (T6P) or Trehalose and their biosynthetic enzymes formed a complex interaction networks with other hormone and sugar-induced signaling pathways, which may function at different developmental stages. To improve the crop yield, biomass and development, modification of trehalose biosynthesis, either at the level of T6P synthesis, T6P hydrolysis, or trehalose hydrolysis (Ines Delorge *et al*., 2014). In plant trehalose biosynthesis takes place as whole genome sequencing were identified in *Arabidopsis* and the rice genome was found to contain nine TPSs and nine TPPs. Among these, functionality have been proven by yeast complementation for *Arabidopsis TPS1*, *TPS6*, *TPPA*, and *TPPB*, rice *OsTPP1* and *OsTPP2*, and maize *RAMOSA3* (*RA3)*. (Vogel *et al*., 2001).

T6P plays a central role in regulating carbohydrate metabolism and act as signaling molecules that modulate metabolic and developmental processes in plants (Paul *et a*l., 2008) More specifically, T6P has been shown to regulate sucrose utilization in plants. Transgenic Arabidopsis lines expressing *E. coli TPS* (*otsA*) or *TPP* (*otsB*) genes displayed differences in T6P accumulation and responded differently to exogenous sucrose. In general, the ability of these plants to utilize sucrose, increased with rising concentration of T6P (Schluepmann *et al*., 2004). The rapid increase of T6P in response to exogenous sucrose may be due to an increase in the amount of available glucose-6-phosphate (G6P) and UDP-glucose (UDPG), which have been shown to be important in determining plant growth and biomass accumulation (Meyer *et al*., 2007). Thus T6P indirectly reflects sucrose concentrations and has now been widely accepted as an indicator of sucrose status in plants (Paul *et al*., 2008).

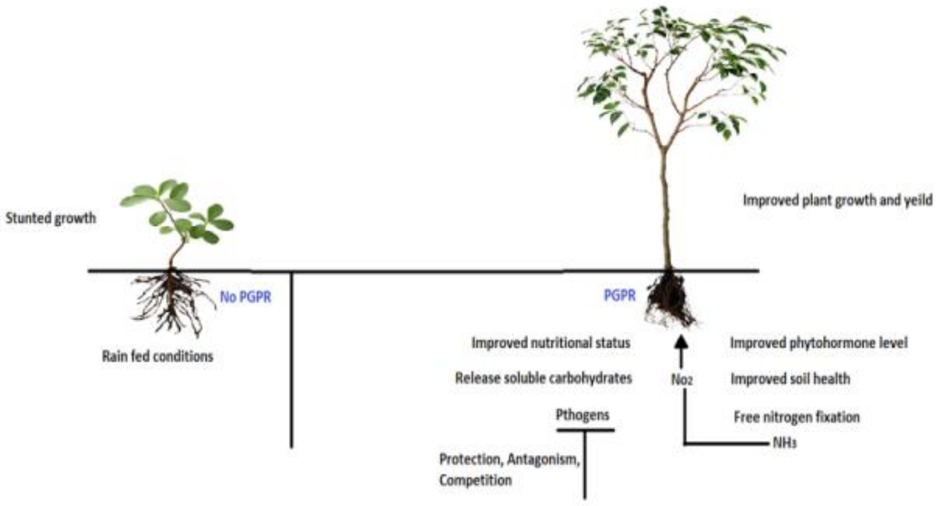

Figure - 2 Plant growth promoting *Rhizobacteria* in drought stress

ROLE OF TREHALOSE IN ABIOTIC STRESS

Trehalose involvement in tolerance to abiotic stress has been found in numerous organisms i.e both prokaryotes and eukaryotes. The effects of abiotic stress are desiccation, salt, high and low temperature stresses have been shown to be averted by trehalose. There are two general mechanisms used for abiotic stress avoidance and adaptation. Avoidance undergoes deeper soil layers where temperature is tolerated in range (Roelofs, 2008). Adaptation stress is based on activation of the stress defense gene pathway which results in production of heat shock proteins, LEA proteins, redox regulating proteins.

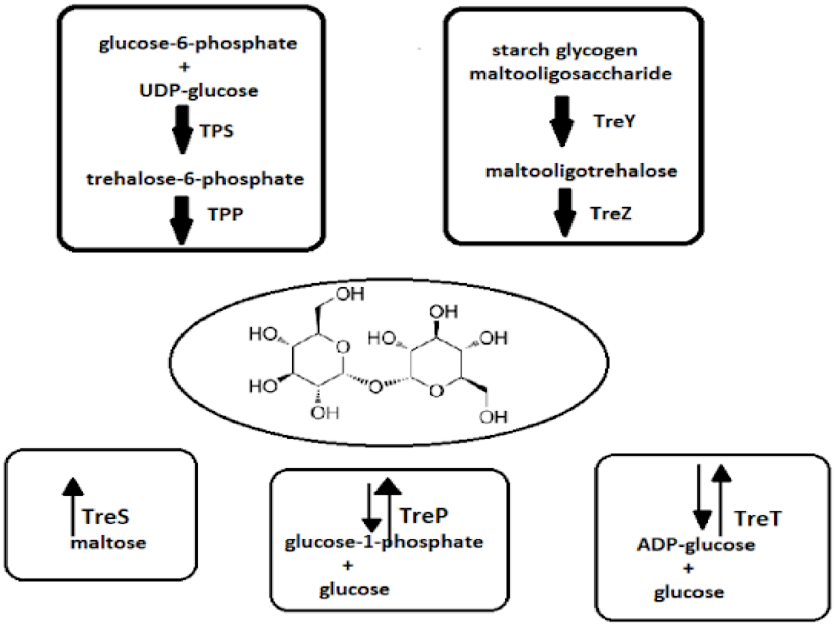

Figure - 3 Biosynthesis of Trehalose

TREHALOSE USES IN RELATION TO ABIOTIC STRESS

To find the stress tolerance in plant it is necessary to propose the stress as usual or unusual biotic or abiotic environment modification that has the capability of causing injury, disease or aberrant physiology. If the plant facing prolonged unfavorable conditions they may recurrent ans shall develop tolerance mechanism to protect from severe damage, the plant synthesizing compatible solute sucrose (Wingler & Roitsch, 2008). Like invertebrates, microorganisms, anhydrobiotic and resurrection plants can able to survive under complete dehydration. These organisms can accumulate high amount of trehalose under dehydration condition (Strom & Kaasen, 1993). Trehalose is the most important of disaccharides is utilized by the plant under desiccation stress able to stabilizing cellular membranes which is the function of vesicle fusion and lipid phase transition.Under dehydration, trehalose accumulation seen in small quantities which reduces vesicle as well as dry lipids transition and maintains their crystalline state (Crowe, 2014). During desiccation and freezing H_2O_2 molecule and it has the property of binding OH molecule with polar groups of proteins and phosphate groups of membranes (Kawai *et al.*, 1992). This process of vitrification is another attribute of trehalose for stress tolerance. Due to non - reducing character trehalose is more stable than other disaccharides. This property leads to holding the molecule firmly and returning bounded molecules to their native structure on rehydration (Crowe, 2014). The glassy structure of trehalose is stable, so that a small amount of water dehydrates the outer surface and protects the internal structure of the plant (Richards *et al.*, 2002).

INFLUENCE OF HEAVY METALS IN THE RESPONSE OF PLANT TO BIOTIC STRESS

Heavy metal stress has become a major concern in various terrestrial ecosystems worldwide. Detrimental effects on soil as well as on crop productivity by accumulating heavy metals by extensive industrialization(Shahid *et al.*, 2015). Figure - 4 depict the influence of heavy metals in the response of plant to biotic stress. Reduction of plant growth adversely affecting various physiological and molecular activities of plants due to damage to soil texture, i.e., pH of soil, presence of different elements, and accumulation of heavy metals (Hassan *et al.*, 2017). Heavy metals such as Zn, Cu, Mo, Mn, Co, and Ni are essential for crucial biological processes and developmental pathways (Shahid *et al.*, 2015). Along with these metals four other are highly toxic heavy metals which includes, arsenic (As), lead (Pb), cadmium (Cd), mercury (Hg), Cr, Al, and Be. These toxic heavy metals can reduce the crop productivity to a great extent when their concentration rises beyond supraoptimal values (Pierart *et al*., 2015). These toxic elements cause metabolic disorders and morphological abnormalitiest lead to yield reduction in plants (Amari *et al*., 2017). These abnormalities also give rise to the production of reactive oxygen species (ROS), e.g., superoxide anion radical (O_2^-), H_2O_2, and hydroxyl radical (OH^-), resulting in disruption of the redox homeostasis of cells (Ibrahim *et al*., 2015). The major cause of heavy metal toxicity in plants is due to this redox status misbalance . To withstand heavy metal stress and metal toxicity, plants have evolved numerous defense mechanisms viz reduced heavy metal uptake, sequestration of metal into vacuoles, binding to phytochelatins/metallothioneins, and activation of various antioxidants (Shahid *et al*., 2015).

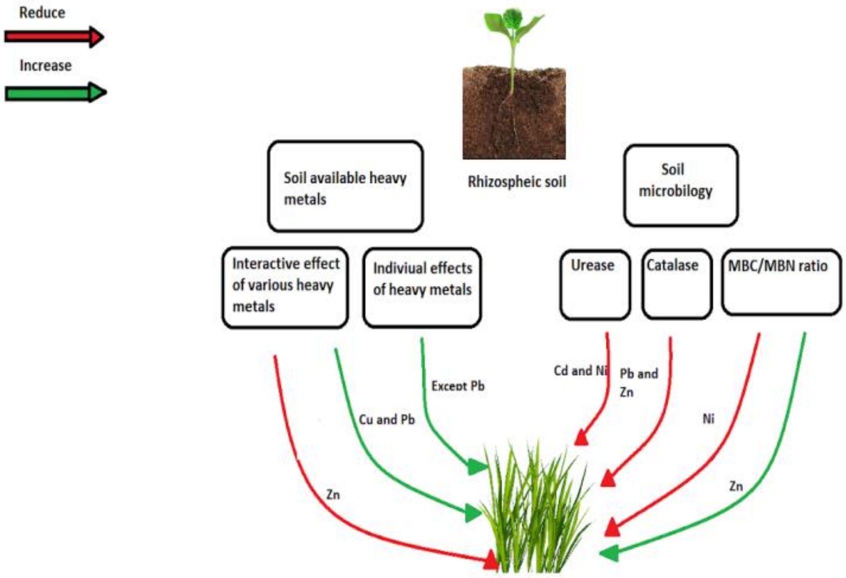

Figure - 4 Influence of Heavy Metals in the response of plant to Biotic Stress

CONCLUDING REMARKS

Due to the current climatic scenario and adverse changes in environment it is difficult for plants to sustain the harsh environment and may lead to drastic drop off in quality and quantity of crop yield. The affirmative properties of trehalose helps to overcome this problem. It can be used as direct foliar application to crops or as a constituent in fertilizers which will show a good result, it also helps the plants to overcome different types of abiotic stresses mainly drought stress, salinity stress. And also using bioinoculants, the crop plants will be benefited in many aspects related to acquiring resistance to many diseases, stress management, increase in rate of uptake of nutrients, and increase in production of Phyto hormones.

Conflict of Interest

The authors declare that they have no conflict of interest.

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