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MITIGATING ABIOTIC STRESS IN CROP PLANTS BY MICROORGANISMS

ABSTRACT: Microorganisms could play an important role in adaptation strategies and increase of tolerance to abiotic stresses in agricultural plants. Plant-growth-promoting rhizobacteria (PGPR) mitigate most effectively the impact of abiotic stresses (drought, low temperature, salinity, metal toxicity, and high temperatures) on plants through the production of exopolysaccharates and biofilm formation. PGPR mitigate the impact of drought on plants through a process so-called *induced systemic tolerance* (IST), which includes: a) bacterial production of cytokinins, b) production of antioxidants and c) degradation of the ethylene precursor ACC by bacterial ACC deaminase. Symbiotic fungi (arbuscular mycorrhizal fungi) and dual symbiotic systems (endophytic rhizospheric bacteria and symbiotic fungi) also tend to mitigate the abiotic stress in plants.

KEY WORDS: adaptation, microorganisms, plant, soil, stress

INTRODUCTION

Abiotic stresses affect the productivity of agricultural crops as well as the microbial activity in soil. Extreme conditions such as prolonged drought, intense rains flooding, high temperatures, frost and low temperatures, which are expected to intensify in the future due to climate changes, will significantly affect plants and soil microorganisms.

Microorganisms could play an important role in adaptation strategies and increase of tolerance to abiotic stresses in agricultural plants. Plant-growthpromoting rhizobacteria (PGPR) are associated with plant roots and mitigate most effectively the impact of abiotic stresses (drought, low temperature, salinity, metal toxicity, and high temperatures) on plants through the production of exopolysaccharates and biofilm formation. When plants are exposed to stress conditions, rhizospheric microorganisms affect plant cells by different mechanisms like induction of osmoprotectors and heat shock proteins.

During the crop production, microorganisms can be used for (a) monitoring of biological activity in soil (microbial number, enzymatic activity and biodiver-

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sity); (b) as indicators of soil health/quality; (c) for mitigation of negative stress caused in plants by abiotic factors; and (d) as beneficial and effective microorganisms as inoculants (G r o v e r et al., 2010, K a s t o r i et al., 2006, M i l o s e v i c et al., 2008).

ADAPTATION OF MICROORGANISMS AS A RESPONSE TO ABIOTIC STRESSES

A large number of environmental factors affect the microbial communities in soil. Some factors are referred to as *modulators* (B a s l e r et al., 2001), in contrast to the *resources* needed for the growth of microbial communities (e.g., carbon, nitrogen). For example, soil temperature, pH, salinity, and water potential are considered as modulators. Plant and microbial communities change in response to stress conditions and there develop new, tolerant communities, adapted through complex regulatory processes involving many genes (M i l o š e v i ć and M a r i n k o v i ć, 2011).

Soil microbial communities consist of many populations, each with a characteristic response curve to a particular environmental factor, indicating the community's physiological flexibility. Changes in the environment may change the composition and biomass of a microbial community. All microorganisms have a set of optimal environmental conditions, which secure their optimal growth (P e t t e r s o n, 2004).

When exposed to stress (drought, excess moisture, high and low temperatures, metal toxicity), most microorganisms have the ability to survive in the soil in an inactive state, but their activity is restored under favorable conditions. Poor and/or degraded soils are inhabited by a narrow range of microbial genera and species, which is reflected on soil fertility and the growth of plants.

Prolonged exposure to stress and the impact of recurring stress factors (stress on stress) impacts the number of microbes in the soil, but not necessarily their metabolic activity (G r i f f i t h s et al., 2000). Each bacterial species has specific growth dynamics which is highly sensitive to environmental factors and it is a more reliable indicator of stress than metabolic activity (B l o e m and B r e u r, 2003; R a j a p a k s h a et al., 2004). Experiments have shown that respiration may increase or decrease in response to stress (T o b o r - K a p ł o n et al., 2006), indicating that it is not a reliable stress indicator. In a study of R a j a p a k s h a et al. (2004), addition of 128 mg of Zn/kg of soil reduced microbial respiration by 30% and microbial growth by 90%. Reduced presence of azotobacters and reduced dehydrogenase activity was registered in soils with a nickel content of 23 to 75 mg/kg of soil. However, a high lead content in the soil inhibited the growth of azotobacters but it did not inhibit soil dehydrogenase activity (M i l o š e v i ć et al., 2008).

Microorganisms are capable of surviving high temperatures caused by fire depending on its duration and intensity. Fires develop high temperatures and cause a rapid loss of water (especially in surface soil layers), changing the soil microclimate, and indirectly affecting the soil microbial community. Most biological reactions are temperature dependent. Exposure to high temperature increases the rates of nutrient decomposition and release. Burning of crop residues in a wheat-soybean rotation did not affect the total number of bacteria and the number of nitrogen-fixing bacteria in soil (H a r r i s et al., 1995). A study of Vázquez et al. (1993) showed that, one month after burning of vegetation cover, the bacterial population was 25 times lower and the number of fungi decreased by about 5% compared with a soil that was not subjected to burning. The population of fungi was reduced in the soils periodically subjected to burning over a period of 10 years (Klopatek et al., 1994, cit. Fites - Kaufman et al., 2006).

Microbial adaptation to stress is a complex regulatory process in which a number of genes are involved (T o b o r - K a p ł o n et al., 2008; G r o v e r et al., 2010). Certain microbial species live in extreme habitats (thermophiles and halophytes) and they use different mechanisms to reduce stress (M a d i g en, 1999; cit. G r o v e r et al., 2010). When subjected to stress conditions, most rhizobacteria produce osmoprotectors (K+, glutamate, trehalose, proline, glycine, and polysaccharates).

MICROORGANISMS: ALLEVIATION OF ABIOTIC STRESSES ON PLANTS

Investigations has shown that certain microbial species and/or strains enhance plant tolerance to abiotic stresses such as drought, salinity, nutrient deficiency or excess (Yang et al., 2008), and high contents of heavy metals (Rajapaksha et al., 2004; Grover et al., 2010; Milošević and Mar i n k o v i ć. 2011). Specifically, rhizospheric microorganisms have the greatest impact on the tolerance of agricultural plants to abiotic stresses. When near plant roots, soil microorganisms trigger different mechanisms that affect plant tolerance to stress. They produce indole acetic acid, gibberellins, and other substances that promote the growth of root hairs and increase total root area, which in their turn facilitate nutrients uptake by plants. Plant-growthpromoting rhizobacteria (PGPR), which live in association with plant roots, elicit the largest influence on plants, affecting their productivity and immunity. PGPR inhabit the rhizosphere of many agricultural plants and they take part in increasing plant growth and reducing diseases caused by pathogenic fungi, bacteria, viruses, and nematodes (K lopper et al., 2004). Yang et al. (2008) introduced the term 'induced systemic tolerance' (IST) that is caused by PGPRs. According to these authors, the mechanism of IST causes physical and chemical changes in plants, which result in plant tolerance to abiotic stresses.

The most important mechanism in many bacteria that directly stimulates plant growth is the production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. Under stress conditions, the bacterial enzyme facilitates the growth of plants by decomposing plant ACC (ethylene precursor in plants). S a l e e m et al. (2007) described the role of ACC deaminase-containing PGPRs in crop production. By reducing the level of ethylene, the plant becomes more resistant to stress conditions in the environment (Glik, 1999).

AM fungi alleviate the effects drought and salinity stresses, osmoregulation and proline accumulation. *Glomus intraradices* increases the tolerance of *Pterocarpus officinalis* to excessive moisture (G r o v e r et al., 2010). In addition, dual symbiotic systems tend to mitigate the effect of abiotic stress on plants. The endophytic fungus *Cuvularia* sp. has been isolated from *Dichathelium lanuginosum* growing on a geothermal soil and showing to be thermotolerant to temperatures of 50°C to 65°C (R e d m a n et al., 2002). When the plant and the fungus grow separately, they do not tolerate temperatures above 38°C.

Drought / excessive moisture

Drought stress limits crop growth and productivity, especially in arid and semi-arid regions. Some microbial species and/or strains that inhabit plant rhizosphere use different mechanisms to mitigate negative effects of drought on plants (Table 1). According to Grover et al. (2010), certain microbial types may mitigate the impact of soil drought through production of exopolysaccharates, induction of resistance genes, increased circulation of water in the plant, and the synthesis of ACC-deaminase, indole-acetic acid and proline.

Crop inoculation (with e.g. *Bacillus amylolequifaciens*) leads to the production of polysaccharates (EPS) which tends to improve soil structure by facilitating the formation of macroaggregates. This in turn increases plant resistance to stress due to water shortage. Soils with a high content of small aggregates contain more nutrients in the form available for plants and microorganisms (NO₃, P₂O₅, K₂O), as indicated by high values of dehydrogenase (M i l o š e v i ć et al., 2002a). However, a high portion of small aggregates causes poor aeration and evacuation of water from soil pores, which leads to a decline in soil fertility in the long run. Macroaggregates are guardians of soil fertility, because they maintain a balance between aerobic and anaerobic conditions and ensure a gradual uptake of nutrients from soil reserves. Inoculation of wheat and sunflower with different species and/or strains of EPS-producing bacteria tended to alleviate drought stress (Table 1).

Microorganism	Crop	Mechanism					
Pantoea agglomerans	Wheat	Production of EPS which affects the structure of rhizospheric soil					
Rhizobium sp.	Sunflower	Production of EPS which affects the structure of rhizospheric soil					
Pseudomonas putida -P45	Sunflower	Production of EPS which affects the structure of rhizospheric soil					
Azospirilum sp.	Wheat	Increased water circulation					
Achromobacter piechaudii ARV8	Tomato Pepper	Synthesis of ACC-deaminase					

Tab. 1. - Effect of microorganisms on drought mitigation in crops

Variovorax paradoxus	Pea	Synthesis of ACC-deaminase					
Pseudomonas sp.	Pea	Decreased ethylene production					
AM fungi	Sorghum	Increased water circulation					
Brome mosaic virus	Rice	Unknown					
Pseudomonas mendocina and Glomus intraradices	Lettuce	Increased antioxidative status					
<i>Bacillus megaterium</i> and <i>Glomus</i> sp.	Clover	Production of indole acetic acid and proline					

Source: Grover et al. (2010)

PGPR mitigate the impact of drought on plants through a process socalled *induced systemic tolerance* (IST) which includes: a) production of cytokinins, b) production of antioxidants and c) degradation of the ethylene precursor ACC by bacterial ACC deaminase. (a) The production of cytokinins causes the accumulation of abscisic acid (ABA) in leaves, which in its turn results in the closing of stomata (F i g u e i r e d o et al., 2008; C o w n et al., 1999; cit. Y a n g et al., 2009). (b) The production of antioxidants (e.g., the enzyme catalase) causes the degradation of reactive forms of oxygen. (c) The bacterial-produced ACC deaminase degrades the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) (Y a n g et al., 2009).

Oxygen is essential for the life on Earth. It is used by all aerobic organisms for the production of energy by the process of respiration. In the course of respiration, oxygen is reduced to water while complex organic molecules (lipids, carbohydrates, proteins) are subject to oxidative degradation. Of the total amount of oxygen in cells, only a small portion (2%-3%) is transformed into toxic forms that are referred to as reactive oxygen species (ROS). Homeostasis in plant cells is maintained for as long as there is a balance between the production of ROS and antioxidants. When exposed to drought stress, some rhizobacteria produce antioxidants which neutralize the toxic effects of ROS in plant cells, reducing damage to cells and biomolecules to a minimum (G o v e r et al., 2010).

Plant inoculation with ACC-deaminase-containing rhizobacteria causes root elongation and water uptake from deeper soil layers, which is reflected on plant growth and development especially under drought conditions (Z a h i r et al., 2008; cit. G o v e r et al., 2010).

Our investigation on the effect of soybean seed inoculation with five *Bradyrhizobium japonicum* strains under three drought levels of conditions showed that differences existed in the reduction of dry matter in plants (Table 2). The soybean plants inoculated with the strains D 216 and 2b plants were most tolerant to soil drought. On average for all three drought levels, the lowest dry weight reduction was registered in the plants inoculated with the strain D 216 (10.05%).

Soybean seed inoculation with five *Bradyrhizobium japonicum* strains under three drought levels resulted in uneven reduction of nitrogen in the aboveground plant parts (Table 3). On average for all three drought levels, the lowest nitrogen reduction in the aboveground plant parts was recorded in the

Day of the second	Bradyrhizobium japonicum (strain)									
Drought intensity	D 216		518		511		2b		1b	
	g	%	g	%	g	%	g	%	g	%
Ø	7.316	100	7.304	100	6.007	100	7.089	100	7.520	100
V 2	7.113	97.15	6.996	95.60	5617	93.06	6.509	91.09	6.781	89.10
V 3	6.454	86.64	6.334	84.69	5.333	87.36	6.379	88.87	6.539	85.00
V 4	6.421	86.06	6.241	82.97	4.892	77.21	6.254	86.65	6.431	83.07
AVERAGE V2-V4	6.663	89.95	6.524	87.75	5.281	85.88	6.381	88.87	6.584	85.72

Tab. 2. – Effect of *Bradyrhizobium japonicum* inoculation on dry matter weight (g) in soybean plants grown under three drought levels (M i l o š e v i ć and M a r i n k o v i ć, 2011)

plants inoculated with the strains 1 b and 511 (3% and 7%, respectively), as compared with the control variant. The results presented in Tables 2 and 3 indicate the possibility of selection and application of microbial strains in the production of soybean under drought conditions.

Tab. 3. – Effect of *Bradyrhizobium japonicum* inoculation on nitrogen content (%) in soybean plants grown under three drought levels

Due altriatenti	Bradyrhizobium japonicum (strain)									
Drought intensity	D 216		518		511		2b		1b	
	% N	%	% N	%	% N	%	% N	%	% N	%
Ø	2.188	100	2.128	100	1.268	100	2.214	100	2.124	100
V 2	1.948	89	1.840	86	1.256	99	1.957	88	2.001	94
V 3	1.995	91	2.020	95	1.149	90	1985	90	2.096	98
V 4	2.040	93	1.990	93	1.160	91	2.007	91	2.090	98
AVERAGE V2-V4	1.994	91	1.950	91	1.188	93	1.983	90	2.062	97

Under conditions of excessive moisture, microorganisms take up the available oxygen while toxic substances accumulate in the soil. In such conditions, plants reduce the permeability of roots, water absorption and nutrients uptake, which reduce the growth of aboveground plant parts and roots. Provoked by excessive moisture, roots release large quantities of aminocyclopropane carboxylate-1 (ACC) into the soil. Some groups of bacteria degrade ACC and reduce its concentration in the soil by secreting the enzyme ACC-deaminase. In excessively moist soil, bacteria such as Enterobacter cloacae and Pseudomonas putida predominate over fungi and actinomycetes (G r i c h k o and G l i c k, 2001).

Mycorrhizal fungi mitigate the stress caused in plants by excessive moisture (S a i n t - E t i e n n e et al., 2006, cit. G r o v e r et al., 2010). It is hypothesized that, under conditions of excessive moisture, the accumulation of acetaldehyde and the high toxicity of ethanol intermediates in roots are responsible for damage to sensitive plant species.

Temperatures

High temperature promotes plant growth and development, while low temperature is the most important limiting factor to the productivity and geographic distribution of agricultural crops.

Some bacterial species and strains affect plant tolerance to high temperature (G r o v e r et al., 2010). So, *Pseudomonas* sp. strain NBRI0987 causes thermotolerance in sorghum seedlings, which consequently synthesize high molecular weight proteins in leaves thus increasing the plant biomass. The bacterium Burkholderia phytofirmans PSJN colonizes grapevine residues and protects the plant against heat and frost through increases in the levels of starch, and proline and phenols. Inoculation of wheat seeds with Serratia marscescens, strain SRM, and Pantoea dispesa, strain 1A increases the seedlings biomass and nutrients uptake at low temperatures.

Salinity

Microorganisms use different mechanisms to alleviate the salinity stress in agricultural crops (Tab. 4). Some rhizobacterial strains (PGPR) affect the growth and development of tomatoes, peppers, beans, and lettuce grown in saline environments (G r o v e r et al., 2010; Y i l d i r i u m and T a y l o r, 2005). Inoculation of wheat seedlings with bacteria that produce exopolysaccharates (EPS) affect the restriction of sodium uptake and stimulation of plant growth under conditions of stress caused by high salinity (A s h r a f et al., 2004, cit. G r o v e r et al., 2010). Corn, beans and clover inoculated with AM fungi improved their osmoregulation and increased proline accumulation which resulted in salinity resistance (F e n g et al., 2002, cit. G r o v e r et al., 2010).

Microorganism	Crop	Mechanism					
Achromobacter piechaudii	Tomato	Synthesis of ACC-deaminase					
Piriformaspora indica	Barley	Increased antioxidative capacity					
AM fungi	Sorghum Corn Clover	Increased water circulation Improved osmoregulation and proline accumulation					
B. amylolequifaciens	When	Restricted Na+ uptake					
Rhizobium and Pseudomonas	Wheat	Restricted Na+ uptake					

Tab. 4. - Effect of microorganisms on mitigation of salinity stress in agricultural crops

Source: Grover et al. (2010)

Heavy metals

Heavy metals affect the soil microbial population, their effects depending on the element in question and its concentration on one side and the bacterial species/strain on the other. Some heavy metals are essential micronutrients that are required in small quantities for the growth of microorganisms and plants. Microorganisms bind soluble heavy metals in three ways (biosorption, bioaccumulation, and the binding by metabolic products), which indirectly reduce the negative impact of heavy metals on plants (G o v e d a r i c a et al., 1997).

Studies have shown that the effect of nickel on the microbiological soil properties depended on the microbial group and agricultural plant species (K a s t o r i et al., 2006, M i l o š e v i c et al., 2002). *Methylobacterium oryzae* and *Burkholderia* sp. reduce nickel and cadmium stress in tomato by reducing their uptake and translocation (M a r q u e z et al., 2007; M a d h i y a n et al., 2007). Inoculation with rhizobacteria alleviates abiotic stresses to plants caused by drought, salinity and metal toxicity (D i m k p a et al., 2009). These authors pointed out that the bacteria that are used as biofertilizers are at the same time plant bioprotectants against stress. This interaction between plants and rhizobacteria (e.g., *Bacillus*) mitigates stress conditions. Heavy metals such as Cd, Ni, and Pb disrupt the water regimen in plants. Proline accumulation in plant cells is a biomarker for stress induced by heavy metals.

The symbiotic associations between *Rhizobium/Bradyrhizobium* and leguminous plants are sensitive to the presence of heavy metals in soil (G o v e d a r i c a et al., 1997). Heavy metals tend to inhibit nodulation. i.e., they interrupt the rate of symbiosis between plants and mikrosymbionts depends on heavy metals concentration in soil.

CONCLUSION

Microorganisms help agricultural plants to increase their tolerance and adaptation to abiotic stresses. The complex and dynamic interactions between microorganisms and plant roots under conditions of abiotic stress affect not only the plants but also the physical, chemical, and structural properties of soil. The possibility of mitigation of abiotic stresses in plants opens a new chapter in the application of microorganisms in agriculture. Some microbial species and strains could play an important role for understanding plant tolerance to stress, adaptation to stress, and mechanisms that develop in plants under stress conditions. Selection of microorganisms from stressed ecosystems may contribute to the concept of biotechnology application in agriculture.

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УТИЦАЈ МИКРООРГАНИЗАМА НА УБЛАЖАВАЊЕ ПОСЛЕДИЦА АБИОТИЧКОГ СТРЕСА КОД ПОЉОПРИВРЕДНИХ КУЛТУРА

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Резиме

Микроорганизми могу имати значајну улогу у стратегијама адаптација и повећању толерантности пољопривредних биљних врста на абиотичке стресове. Највећи утицај ублажавања абиотичких стресова на биљку (суша, ниске температуре, салинитет, токсичност метала и високе температуре) имају микроорганизми који насељавају ризосферно земљиште, а промотери су биљног раста (ПГПР), кроз продукцију егзополисахарида и формирањем биофилма. ПГПР ублажавају утицај суше на биљке *индукованим сисшемом шолеранције* (ИСТ): а) продукцијом бактеријског цитокинина б) продукцијом антиоксиданата и ц) деградацијом етилен прекурсора АЦЦ бактеријским АЦЦ-деаминазом. Такође и симбиозне гљиве (abscular mycorrhizal fungi) и дуал симбиозни системи (rhizosphere, endophytic bacteria и symbiotic fungi) утичу на ублажавање абиотичких стресова у биљкама.

КЉУЧНЕ РЕЧИ: адаптација, биљка, земљиште, микроорганизми, стрес