

Abstract of Ph.D. thesis

Effect of salicylic acid pre-treatment on salt stress acclimation particularly on
the role of glutathione transferases in tomato and *Arabidopsis* plants

Edit Horváth

Supervisor:

Dr. Jolán Csiszár

associate professor

Biology Ph.D. School

University of Szeged

Faculty of Science and Informatics

Department of Plant Biology



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INTRODUCTION

Plants can be affected by many stress factors which are either biotic or abiotic stressors. Salt stress is one of the major abiotic stresses, which can affect almost every aspect of the physiology and biochemistry of plants resulting in reduced growth and yield, accelerated development, senescence and even death, so it is very important to understand the acclimation processes of plants during salt stress.

There are different kinds of solutions to decrease the reduction of productivity, one of them is the selection of stress resistant genotypes. To increase the efficiency of breeding a better understanding of the stress response of plants is essential and the identification of genes important in stress tolerance is needed. However, beside the breeding techniques, scientists are looking for other methods to increase the stress tolerance of plants. Salicylic acid (SA) has been known as priming molecule for more than 20 years, and exogenous application of it can be an alternative solution. It was known that exogenously applied SA can induce salt stress resistance, but it has been proven that this effect depends on the plant's developmental phase, the way of the treatment and the used concentrations.

In previous studies abscisic acid (ABA) was found to play an important role in the positive effect of SA pre-treatment during salt stress acclimation of tomato (*Solanum lycopersicum*) plants. In the present work we investigated the activity of some enzymes involved in ABA biosynthesis and the expression levels of selected key genes in tomato. Furthermore, our aim was to study the effect of SA pre-treatment used in wide concentration range and long-term on *Arabidopsis thaliana*. As a genetic model plant, *Arabidopsis* offers a good tool to reveal the background of the processes. We applied a hydroponic system in our experiments and the effects of long-term SA pre-treatments and subsequent salt stress on the plants growth, reactive oxygen species (ROS) content and lipid peroxidation were investigated. We compared the changes in antioxidant enzyme activities after the salt stress treatment of SA-pre-treated and untreated plants. The GST enzyme family plays an important role in the alleviation of secondarily appearing oxidative stress, thus glutathione transferase (GST) and glutathione peroxidase (GPOX) activities and the changes of expression of several *AtGST* genes were studied. Two *AtGST* mutants have been chosen (*Atgstf9* and *Atgstu19*) to study the effect of

mutation of one GST gene on stress responses after short-term SA- or NaCl-treatment. Furthermore, we studied the role of GSTs, changes in the GST activity- and expression pattern due to SA pre-treatment in tomato.

AIMS

In the dissertation we were looking for answers to the following questions:

In long term experiments of *Arabidopsis thaliana* L. plants:

1. How do the different SA concentrations affect the growth and other physiological parameters of *Arabidopsis* plants? How does long-term pre-treatment influence the subsequently induced salt stress response of plants? What kind of changes does SA induce in enzymatic antioxidant activities and in which manner does SA influence the salt stress response?
2. Which SA concentrations induce priming of plants and what kind of physiological changes can be described in connection to successful acclimation?
3. How do GST and GPOX activities change under pre-treatment and subsequently triggered salt stress? Is there any correlation between the changes measured in GST activities of plants and the expression of GST genes?

Short-term experiments of *Arabidopsis thaliana* L. *GST* mutant plants:

4. Does the mutation of a single *GST* affect the viability and GST activity of plants under control conditions or NaCl- and SA-treatments? What kinds of phenotypic changes can cause the mutation of one *GST* gene under high salt- and SA treatment?

In experiments carried out on *Solanum lycopersicum* Mill. L. cvar. Rio Fuego:

5. What kinds of changes induce the SA priming in tomato plants' GST and GPOX activities? Is there any connection between the differences measured in activities and the expression of GST genes?

6. Can the changes of ABA levels be explained by the differences measured in AO activities and the expression of ABA biosynthesis genes?
7. What similarities and/or differences exist in the two species in the phenomenon of SA pre-treatment induced priming and in salt stress acclimation?
8. Would it be possible to find any correlation between the investigated GST gene expressions and the *cis*-acting regulatory elements of 5'-end regulatory regions? How similar are the regulatory regions of ortholog sequences?

MATERIALS AND METHODS

5-week-old *Arabidopsis thaliana* L. plants were treated hydroponically with a 10^{-9} - 10^{-5} M SA concentration range in the long-term experiments for 2-weeks and subsequently with 100 mM NaCl for one week. In case of *Solanum lycopersicum* Mill. L. cvar. Rio Fuego the plants were grown in a hydroponic system as well. Four-week-old tomato plants were pre-treated with 10^{-7} and 10^{-4} M SA for 3 weeks and after that the hydroponic medium was supplemented with 100 mM NaCl for 1-week.

In the case of *Arabidopsis thaliana* L. wild type and GST mutant (*Atgst19* and *Atgst9*) seedlings, 2-week-old seedlings were treated with 10^{-5} M SA or 150 mM NaCl on $\frac{1}{2}$ MS medium for 48 h, or – in order to compare the growth in the presence of stressors - 4-day-old seedlings were grown on plates containing SA- or NaCl for 2 weeks.

We measured the root- and shoot length of plants, and the changes in the biomass of the roots and leaves during the treatments. The sodium and potassium contents were determined by inductively coupled plasma mass spectrometry (ICP-MS). The viability and ROS content were investigated by fluorescent microscopy. The H_2O_2 and malondialdehyde content, the antioxidant enzyme activities, such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (POD), glutathione transferase (GST), glutathione peroxidase (GPOX) and dehydroascorbate reductase (DHAR) activities were detected using spectrophotometric methods. The native-polyacrylamide gel electrophoresis method was used to determine the aldehyde oxidase (AO) activity.

Gene sequences were identified *in silico* and a homology tree was constructed using ClustalW, MEGA5 and Dendroscope 3 programmes. *In silico* analyses of promoter regions were done in PlantCARE database on the 1.5 kbp length 5' UTR region of the genes. RNA was isolated using the TRI method for gene expression analyses and primers designed using Primer3 software were applied in quantitative RT-PCR experiments.

The statistical analyses of the data were processed and evaluated in SigmaPlot 11.0 (Systat Software Inc, USA) software.

RESULTS AND DISCUSSION

In our experiments the components of the salicylic acid (SA) pre-treatment triggered changes in salt stress acclimation was studied and based on our results they can be summarised as followed:

In *Arabidopsis thaliana* L. plants during the long-term experiments it was found:

1. Wide range of SA concentrations (10^{-9} - 10^{-5} M), similarly to data in the literature, affected the shoot and root growth of *Arabidopsis* plants on a concentration dependent manner. SA stimulated the growth of shoots, and pre-treatment with higher (10^{-6} and 10^{-5} M SA) concentrations proved to be effective in preventing the growth inhibition under salt conditions . SA treatments affected the content of Na and K elements in leaves and roots, and during salt stress the SA pre-treatment facilitated the uptake of K, reduced the Na accumulation of roots, however it induced the Na accumulation in leaves. The 10^{-6} and 10^{-5} M SA elevated the K/Na ratio in roots which could approve the growth of roots. Furthermore, the SA pre-treatment reduced the H₂O₂ and malondialdehyde (MDA) contents in *Arabidopsis*. As a result, the 10^{-5} M SA pre-treatment could induce priming and improved the growth of plants during salt stress which plays key role in successful acclimation.
2. We found that the antioxidant CAT enzyme activity decreased in roots and leaves, SOD activity was on control level and POD activity increased in roots of 10^{-6} and 10^{-5} M SA treated plants. SA affected the response of antioxidant enzymes during salt

stress in a concentrations-dependent way. Salt treatment enhanced the POD activity in the roots and induced the SOD activity in leaves of 10^{-6} and 10^{-5} M SA pre-treated plants. Our results indicate that the higher POD and/or SOD activities in SA pre-treated plants are part of the increased salt acclimation, in 10^{-6} and 10^{-5} M SA pre-treated *Arabidopsis* plants.

3. SA induced the GST and GPOX activities in *Arabidopsis* plants, and 10^{-5} M SA promoted the further elevation of GST and GPOX activities in contrast to salt stress which decreased the GPOX activity. The induction of GST and GPOX activities could be at least partially the results of the induced expression of *AtGSTU19* and *AtGSTU24* genes.

Results of short term experiments of GST mutant *Arabidopsis thaliana* plants:

4. Salt- and SA treatment of *Arabidopsis* GST-insertional mutant seedlings induced changes in the GST activities and root growth from which we may assume that both of the investigated AtGSTs play role in response to high salinity and SA. The reduction of root growth in the mutants refer to the positive role of *AtGSTU19* and *AtGSTF9* isoenzymes in the salt stress response, probably through the regulation of detoxifying processes and in this way favour the maintenance of cells homeostasis and the growth of plants.

Main results of the experiments carried out on *Solanum lycopersicum* Mill. L. cvar. Rio Fuego plants:

5. Priming with 10^{-4} M SA pre-treatment of tomato plants also induced the GST and GPOX activities after one week of salt stress. The expression of *SIGSTF4* and *SIGSTU26* genes in leaves and the transcript level of *SIGSTT2*, *SIGSTZ2* and *SIGSTL3* genes in roots increased, thus these genes could contribute to the elevated GST and GPOX activities and may be important in the induction of elevated salt tolerance.

6. The changes detected in the levels of ABA could be explained by the result of the different AO activities and the changes detected in the expression of ABA biosynthesis genes. SA induced the ABA biosynthesis gene expression during the pre-treatment period, mainly in roots, but only the 10^{-4} M SA concentration induced the accumulation of ABA in leaves. Although ABA biosynthetic genes were down-regulated or the AO activity was inhibited in 10^{-4} M SA pre-treated plants under salt stress, the ABA level was kept over the untreated control (Szepesi et al., 2009). These results suggest a reduced ABA degradation in hardened plants. It can be concluded, that priming of tomato with SA against salt stress injury is a complex phenomenon, which along with fine tuning of the accumulation of ABA comprises other SA- and ABA signalling-dependent processes.
7. Although the SA-induced priming affected differently the growth of the two investigated plant species (in tomato the 10^{-4} M SA decreased, in *Arabidopsis* 10^{-5} M SA concentration enhanced it), during salt stress both species had longer roots and shoots, which could be explained at least partially with the similar changes detected in the Na and K contents (the K and Na contents of tomato was published earlier in Szepesi et al. 2009). The pre-treatments reduced the accumulation of H_2O_2 and MDA in *Arabidopsis*, similarly to that of detected in tomato (Gémes et al. 2011). These results suggest that SA-mediated acclimation can reduce oxidative damage caused by salt stress through modulating activities of some of the key ROS- and peroxide detoxifying enzymes. In this process the antioxidant enzymes and the GSTs play important role both in tomato (Szepesi et al. 2009, Tari et al. 2015) and in *Arabidopsis*. After the priming, the GST and GPOX activities increased in both plant species and the *GST* gene transcript levels had specific pattern during the subsequent salt stress. *GST* genes with induced expression during the priming were identified both in tomato and *Arabidopsis*, thus it could be conclude that at least some of the alterations in enzyme activities derive from modulation of transcriptional control of key detoxification genes.
8. The investigation of 5' promoter region of GST genes revealed that the gene expression is under complex regulation, and clear correlations between the presence

of certain elements and the regulation of the expression were not found. The regulatory elements of promoter region of orthologous sequences could be very distinct, thus the similarities of the genes are not sufficient to make a general conclusion about the pattern of gene expression in different plant species.

(*Present thesis is based on articles marked by an asterisk)

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